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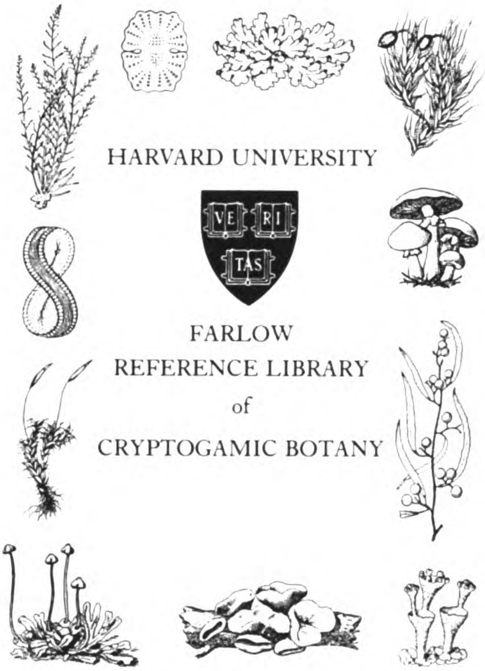

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OHIO BIOLOGICAL SURVEY

BULLETIN 5
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THE ASCOMYCETES OF OHIO, I

Preliminary Consideration of Classification

BRUCE FINK

THE ASCOMYCETES OF OHIO, II

The Collemaceae

BRUCE FINK AND C. AUDREY RICHARDS

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THE ASCOMYCETES OF OHIO.—I

PRELIMINARY CONSIDERATION OF CLASSIFICATION*

BRUCE FINK

All classifications of ascomycetes hitherto followed have been highly artificial, nor are the data for a satisfactory disposition at hand. Hitherto, these fungi, except for lists from two states and certain works mentioned in this paper, have been placed in two groups. In the work to follow, all the ascomycetes of Ohio will be treated as a single class of fungi, and some defense of this method is in order.

The reasons for treating ascomycetous lichens and other ascomycetes together involve mainly the following three considerations: first, the nature of the lichen in general; second, a review of the similarity of lichens and other ascomycetes; third, a discussion of the origin of all ascomycetes, with a view to showing relationships within the group. These three matters will be treated in order and as briefly as is consistent with clearness. Frequent reference will be made to other papers where more lengthy discussions of certain phases of the problem may be found.

Until the time of Schwendener (57), it was generally believed that the chlorophyllous cells found in lichens were the chloroplasts of these plants. Bornet (12) grew lichens from spores in cultures and saw them attack algæ. Bonnier (11), by similar methods, obtained mature fruited plants of *Xanthoria parietina* and *Rinodina sophodes*. Möller (47) followed by growing *Calicium parietinum* in cultures without algæ and obtained plants that produced spermagonia and probably archicarps as well. Fink (31) has reported on the frequent growing of various algal hosts in the same habitats with lichens.

Had it not been for clinging to erroneous tradition, the researches referred to above and others like them would have convinced all botanists that the lichen is a fungus living in some peculiar relation with an alga. Unfortunately, Reinke (53), Schneider (55), and others have aided in retarding progress, and a considerable number of botanists still cling to some modification of the early view. Peirce (52), Elenkin (25), and Danilov (20), with their researches which greatly strengthen belief in the parasitism or the saprophytism of lichens on algæ, have succeeded in turning the attention of botanists toward more plausible conclusions.

We need only to advance definitely to the widely but rather hazily understood idea that the lichen is a fungus, the alga being its host and therefore forming no part of it. Some of the arguments for this position may be reviewed briefly. The algal host is in a disadvantageous position with respect to light and food materials. The cells of the host become large and may divide rapidly because of undue stimulation, showing a hypertrophied and pathologic condition, resulting in marked vegetative activity, which balances the rapid killing of the algal-host individuals. The bright-green, normally-shaped, algal individuals seen in lichens are usually those that are not yet parasitized, or those that have been recently parasitized. The relationship between the lichen and the alga is peculiar on account of the simple structure of the latter; but the lichen seems to be a parasite or a saprophyte, or perhaps partly a parasite and partly a saprophyte, on the alga. The haustoria of lichens are similar to those of other fungi and in all probability function in like fashion. For an extended discussion, see the paper by Fink (31).

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* Contributions from the Botanical Laboratory of Miami University—XI.

One cannot deal with colonies in studies of ontogeny, phylogeny, morphology, or taxonomy, nor does the use of *Collema pulposum*, *Physcia stellaris*, or other binomial by one group of botanists to designate a plant and by another group to designate a compound colony conduce to clearness. In order that one may be clear in his thinking regarding lichens, he must abandon the historical idea that the chlorophyllous cells found in these plants, or in which the lichens live in a few instances, are part of the lichen, or he must hold consistently to the view that the lichen is not a plant, but a compound colony. Critical examination of statements about lichens by a large number of botanists shows that it is not possible to regard the lichen in one of these ways for one purpose and in another manner for another purpose, or even to consider the compound colonies for one purpose and the fungi of the colonies for another purpose, without committing some of the inconsistencies so commonly found in statements about lichens (see discussion in Fink 31). The conclusion that the lichen is a fungus is the only one that can be followed equally well by the physiologist, the ecologist, the morphologist, the cytologist, and the systematist. In a previous paper (Fink 31), the typical lichen has been defined as a fungus which lives in parasitic relationship with an alga during all or part of its life, and also sustains a relationship with an external substratum, organic or inorganic. The lichens will be dealt with according to this definition in the treatment of the ascomycetes throughout this series of papers.

Lichens possess few distinct characters other than physiological, and these have no weight in the classification of these plants. The dual hypothesis can scarcely be considered seriously in view of recent studies

(Fink 31). With this hypothesis falls the argument that lichens constitute a special biological group, nor can classification consistently consider such groups in any event. Some botanists have supposed that we must know the relation of every lichen or every group of lichens to a non-lichen ancestor with some degree of certainty before we attempt to distribute lichens, but this position is manifestly erroneous. Phylogeny is a science of probabilities, and such exact knowledge of relationships has not been attained in any group of plants of considerable size. Lichens resemble other ascomycetes in their methods of sexual reproduction, and their special manner of vegetative reproduction by soredia and soralia can have no considerable weight in favor of treatment as a distinct group of plants. Higher lichens exhibit certain peculiarities of vegetative structure, due to their parasitism on algæ; but their fruits are like those of other ascomycetes, which in turn vary greatly with respect to somatic structure. In view of the facts regarding the reproductive tracts and the fruits, the peculiarities in regard to somatic areas are not sufficient ground for distinct consideration of lichens, especially since they are connected with other ascomycetes by hundreds, if not thousands, of intermediate orders, genera, or species.

Present separate incorporation of lichens in herbaria, the large literature of lichenology, and the fact that students of ascomycetes, for most part, may be divided into two groups, those who study lichens and those who study other ascomycetes, present real obstacles to be overcome; but arguments of expediency and temporary convenience are hardly valid reasons for maintaining a system of classification that is not in accord with present knowledge regarding the structure, the ontogeny, and the probable phylogeny of ascomycetes. For this reason, many botanists who have considered the matter carefully believe that our method of treatment, which is, in spite of temporary inconvenience, in accord with knowledge of the ascomycetes, should be followed in any systematic treatment of the whole group.

There are many genera of ascomycetes which contain some lichen and some non-lichen members, and, as stated above, the bridges that connect ascomycetous lichens with other ascomycetes are many. The best way to facilitate comparison of these forms and thus strengthen our knowledge of the ascomycetes as a whole is to treat the group as a unit. This is, without doubt, also the best way to express what is known regarding these fungi.

Some of the points of nearest approach of lichens to non-lichen ascomycetes are the following. *Endomyces scytonematum* is a lichenoid plant. The genus *Mycocalicium*, of the *Caliciaceae*, has been segregated from *Calicium* to receive members which do not live with algæ. *Sclerotinia tuberosa* is known to live rarely in parasitic relation with an alga (Synes 58). Some of the *Celidiaceae* are algicolous, others not. *Agyrium rufum* has been considered both lichen and non-lichen. The species of *Lecideopsis* seem to be partly lichens and partly non-lichens. Tobler's study of *Phacopsis vulpina* (62) proves that this plant is a lichen, and the species of *Conida* and *Celidium* await similar study. The *Patellariaceae* present similar conditions in that the genera *Karschia, Biatorella, Leciographa,* and *Melaspilea* all contain some algicolous and some non-algicolous ascomycetes. Among the *Lecanactidaceae* are species which are non-algicolous. Zukal's investigation (67) has shown that *Paruphrädria heimerlii* and *Geopezia rehmii* of the *Cenangiaceae* are both algicolous, though other members of the family are non-algicolous. Some species of *Dichaena* are supposed to be lichens, while other members of the *Dichaenaceae* are not. The lichen genus *Arthonia* is well known to contain non-lichen species and other species that are non-algicolous during part of their lives. The same condition is found in the lichen genera *Graphis* and *Opegrapha* (Frank 33), and no one knows how many species are non-algicolous during part or all of their lives, or how many other genera of the *Arthoniaceae* and the *Graphidaceae* contain both lichen and non-lichen members. Further statements regarding forms transitional between lichen and non-lichen ascomycetes will be found in a previous paper (Fink 31), and only extended biological research will give definite knowledge of hundreds or perhaps thousands of such plants which are poorly understood.

The research on the sexuality of ascomycetes is all comparatively recent, nothing of importance dating back of 1863 (De Bary 3). The whole literature of the subject is readily available and is convincing with respect to the rather close relationship among all undoubted ascomycetes. The lichens that have been studied, except those that are degenerate with respect to sexual reproduction, show the *Collema*-like type of female reproductive tract, which is very similar to that found in some other ascomycetes that have been studied. Likewise, most lichens and other ascomycetes agree in that they develop similar ascocarps, simple or compound. It is admitted that the topography, the cytology, and the full development of the sexual reproductive tracts and the ascocarps are not completely known in any of the species that have been studied, and a large amount of research is still necessary before we can hope to approximate a natural classification of ascomycetes. The nuclear behavior is known more or less completely in a considerable number of non-algicolous species, but in only one algicolous species (Bachman 2). Though the results are fragmentary and some of them unreliable, one who considers carefully even the small portion of the research that can be discussed in this paper can scarcely doubt that the ascomycetes form a natural group of fungi.

Through the researches of several botanists, we know something regarding the sexual reproductive tracts and sexual reproduction in lichens (Bachman 1 and 2; Baur 4 and 5; Darbishire 2; Fünfstück 37 and 38; Krabbe 42 and 43; Lindau 44 and 45; Nienburg 50; Schulte 55; Stahl 59; Sturgis 60; Wahlberg 63; Wolff 66; and others). The many-celled archicarp, with its long, many-celled trichogyne and its coiled, septate ascogonium, is quite uniform and recalls conditions found in higher non-lichen ascomycetes, especially certain members of the *Pezizales*, the *Hypocreales*, the *Sphaeriales*, and the *Laboulbeniales*.

One can imagine readily enough how a one-celled ascogonium surmounted by a one-celled trichogyne, as in *Pyronema* (Harper 39), Claussen 16) may be related to the complicated, multicellular, and imperfectly understood female reproductive area of certain lichens and other ascomycetes (Fig. 1, et seq.); but the simpler female tracts usually occur with undoubted antheridia, and these cannot be homologized so easily with the spermagonia usually found in ascomycetes which possess the more highly differentiated female reproductive tracts. Hence, we may also suspect, among those non-lichen ascomycetes that have spermagonia and the more complicated female reproductive tracts, a close relationship with certain of the polyphyletic lichens. Rather unexpectedly, only part of the *Pezizales* examined have furnished types of reproductive tracts so nearly like those of the gymnocarpous lichens examined as have several species of angiocarpous, non-lichen ascomycetes. While the reproductive tracts of a large majority of the *Pezizales* and the *Lecanorales* remain to be studied, we may still expect to find many closely related forms connecting these two orders; but, for the present, usual similarity in the topography of the reproductive areas has been one factor which has led to placing the gymnocarpous lichens, for most part, in a continuous series. Future studies may require more or less modification of this method.

The discussions to follow will further elucidate this matter and will show especially a striking and rather surprising similarity between the reproductive tracts of the *Lecanorales* and the pyrenomycetes in general. *Polystigma rubrum,* whose archicarp has been described and figured

(Fisch 32 and Frank 34), has spermagonia, spermatia, ascogonia, and perhaps trichogynes especially like those found in many of the *Lecanorales*. *Gnomonia crythrostoma* also has given similar results (Frank 35). Working on the former plant, Blackman and Welsford (10) confirmed the findings of Fisch and Frank regarding the female tract in general, but thought that their supposed trichogynes might be vegetative hyphæ which protrude through the stomata, that the spermatia might be functionless, and that the ascogenous hyphæ might arise from somatic tracts (Fig. 3). However, all of these results on *Polystigma* are offset to some extent by Nienburg's results given below. Brooks (13) found in *Gnomonia erythrostoma* spermatia attached to the trichogynes, but thought that both spermatia and trichogynes might be functionless. As was noted by several workers, these reproductive tracts, however degenerate they may be, show in both spermagonia and archicarps a strong resemblance to conditions well known in certain lichens which are considered below. Higgins(41) has recently found in *Sphacrella* very similar appearances, which need further investigation.

It is convenient to call the coils of an ascocarp an ascogonium and the remainder of the structure a trichogyne, but such use of terms is often inexact. Nienburg (51), working on *Polystigma rubrum,* seems to have found that one uninucleate cell of the coiled portion of the archicarp is the ascogonium. A multinucleate cell next the uninucleate cell in the same coil, he regards an antheridium. He finds what he supposes to be functionless trichogynes and spermatia, and regards the antheridium and the method of reproduction respectively a secondarily acquired reproductive organ and a secondarily acquired sexual process. He believes that the ascogenous hyphæ do arise from the ascogonium. The question remains whether he may not have missed a temporary perforation of the transverse septa of the trichogynes and the passage of sperm nuclei through the trichogyne and other cells of the highly differentiated coil to the ascogonium. His paper is remarkably interesting and suggestive and will of course result in a re-examination of the much-studied but still not fully understood *Polystigma rubrum* and many other ascomycetes which have similar reproductive tracts. We must pass over Nienburg's evidence of delayed nuclear fusion and his discussion of probable relationship between the *Ascomycetae* and the *Oomycetae*. In this matter, his views are similar to those of Claussen (16). Recent work by Dodge also sheds light on the real nature of the ascogonium (23 and Fig. 7).

According to Miss Nichols (49), *Ceratostoma brevirostre* has a one-celled, coiled ascogonium, to whose tip an antheridium becomes attached directly. The ascogonium septates after fertilization, and the resulting ascogenous structure (ascogenous hypha?) appears at this stage much like the septate ascogonium of a lichen. Miss Nichols suspected that De Bary might have been mistaken about the ascogonia degenerating and the asci arising independently in *Xylaria,* and that other earlier workers, Hartig (4) and Woronin, might have failed to follow the development carefully in *Rosellinia* and *Sordaria.* If her suspicions are correct, and H. B. Brown (14) has since proved them so for a species of *Xylaria,* conditions found in these non-lichen species are somewhat similar to those known in lichens with respect to the female reproductive tract. If any of the results which indicate that degeneration of the female reproductive tract and the independent origin of ascogenous hyphæ and asci are reliable, such degenerate conditions would be similar to certain degenerate states noted below in certain lichens.

Miss Dawson (22) has also found, in *Poronia punctata,* conditions much like those reported in lichens by several workers. The female reproductive tract consists of a multicellular, coiled hypha surmounted by a more slender, muticellular portion which rises a short distance above the surface of the stroma. In later stages, the supposed ascogonium is absent, and ascogenous hyphæ appear. Miss Dawson could not connect the last two structures, nor did she find spermagonia. However, she considered the female tract similar to that found in lichens, and her figures indicate one of the nearest approaches hitherto discovered among non-algicolous ascomycetes to conditions well known among lichens, at least in regard to appearance of the archicarp.

Ascogonia not accompanied by trichogynes have been reported for *Peltigera, Peltidea,* and *Nephroma* (Fünfstück 37), and it is supposed that, in these plants in which spermagonia are absent or rare, the apothecia arise apogamously (Fig. 8). Baur (5) has reported similar conditions in *Solorina saccata,* and several other lichens have given practically like results (see especially Sturgis 60). All of these lichens show degeneration of the sexual tracts comparable to that found in some of the non-lichen ascomycetes considered above.

Some slightly different conditions among lichens must be noted. The genus *Bæomyces* seems to present conditions similar to those already discussed for other ascomycetes from the results of Brooks, those of Nienburg, and those of Blackman and Welsford. Nienburg (50) has also worked on lichens and found no trichogynes in *Bæomyces,* nor was he sure that he found ascogonia. He thought that the asci might arise either from ascogenous hyphæ or directly from ascogonia. Spermagonia are rare in the genus, and he concluded that the apothecia arise apogamously. In his work on *Sphyridium byssoides,* he found reduced and probably functionless trichogynes, while here again the spermagonia are rare. In this species, however, he succeeded in tracing the origin of ascogenous hyphæ from ascogonia. Reduction of the sexual apparatus does not seem to have proceeded so far here as in *Baeomyces;* but the plant may be apogamous, and, according to Nienburg's results, it is intermediate between *Baeomyces* and those lichens which have normal sexual organs, both male and female. In the *Caliciaceae,* sexual reproductive areas seem to be for most part absent, though Neubner (48) supposed that functionless spermagonia might exist in certain species. Neubner thought that the apothecial development must be wholly vegetative. Mrs. Gertrude Wolff Tobler (66) noted somewhat uncertainly a single transverse septum in the trichogynes of *Graphis elegans,* and we seem to have here a condition intermediate between the unicellular trichogyne of some non-lichen ascomycetes and the typical lichen trichogyne. It is not quite certain whether these simpler archicarps are primitive or degenerate, and more work on the Hysteriales, whether algicolous or non-algicolous, would certainly give other helpful results.

It seems probable that in *Pyrenula nitida* the female sexual tract is perhaps more like the well-developed conditions found in certain discomycetous lichens that have been studied than those of the non-lichen pyrenomycetes that have been examined. Baur's work on *Pyrenula* needs confirmation and extension, since there is room to suspect that the resemblance of the female reproductive tract to the typical, fully developed form found in discomycetous lichens may not be so close after all. Much work is needed on both lichen and non-lichen pyrenomycetes before we can know certainly whether the pyrenomycetous lichens are related more closely to non-lichen pyrenomycetes than to discomycetous lichens.

Conditions among the *Laboulbeniales* (Thaxter 61 and Faull 26 and 27) are considerably like those found in lichens. A complete series from the one-celled trichogyne to a multicellular and much-branched form has been found (Fig. 4). Non-motile male cells become attached to the trichogynes as in lichens, and later the ascogonium septates or in some manner gives rise to a septate structure somewhat similar to the septate ascogonium of lichens. Some of the conditions known in the *Laboulbeniales* appear to be intermediate between those found in *Ceratostoma* and those that have been observed so frequently in lichens.

There are also conditions among the *Pezizales* which strongly suggest the female reproductive tract in lichens. In *Lachnea stercorea,* Fraser (36) found a one-celled ascogonium surmounted by a several-celled trichogyne (Fig. 2). The cells of the female reproductive tract are multinucleate, and the conditions may be intermediate between those found in *Pyronema* (Harper 39 and Claussen 16) and those well known in lichens. In Cutting's (19) discussion of results obtained in a study of *Ascophanus carneus,* it appears that the archicarp consists of a multicellular ascogonium and a multicellular trichogyne comparable to those of lichens. Two recent researches show a strong resemblance between the sex organs of lichens and non-lichen discomycetes. Miss Bachman's results (1 and 2) in a member of the *Collemaceae* (Fig. 6) and those of Dodge (23) in *Ascobolus carbonarius* (Fig. 7) furnish striking resemblances which, if later found to occur often in both algicolous and non-algicolous discomycetes, will demonstrate a much closer relationship between certain gymnocarpous lichens and the *Pezizales* than we are at present showing in our classification. There is good reason for believing that, in many supposed apogamous lichens and in others as well, internal trichogynes and internal spermatia (antheridia?) may occur, and that further studies will give results similar to those obtained by these workers. Among the lichens, some of the promising plants are other members of the *Collemaceae,* some of the lichens supposed to have degenerate reproductive tracts and apogamy, and members of the *Gyalectaceae* and the *Lecideaceae,* which are probably close relatives of the *Collemaceae.*

The various results concerning sexual reproduction among ascomycetes recounted above and others not considered herein surely lend color to the supposition that the ascomycetes are monophyletic; but the difficulty of homologizing the various types of male reproductive organs still remains, somewhat bridged, however, by types of male organs apparently intermediate between spermatia and antheridia, and suggesting a possible relationship with conidia as well. It has been suggested by some workers that all multicellular ascogonia in ascomycetes are post-fertilization conditions, but the evidence is against this view. The multicellular structures that arise after fertilization from a one-celled ascogonium in such ascomycetes as the *Erysibaceae, Gymnoascus,* and *Ceratostoma* seem rather to represent ascogenous hyphæ. If this be true and the ascogonia of lichens and certain other ascomycetes be really many-celled, such post-fertilization areas cannot be homologous with these muticellular ascogonia. It will be seen that this discussion is made with allowance for lack of knowledge, in most instances, whether one cell or more than one of the coil of the archicarp constitutes the ascogonium.

Only a very small proportion of the many groups of ascomycetes has been studied with respect to sexual reproductive areas and life histories in general, and much of the work accomplished is preliminary, fragmentary, unconfirmed, and unsatisfactory. In all present arrangements of ascomycetes, we find occasionally in juxtaposition families or larger groups that have very different reproductive tracts; and further studies are certain to reveal more of this sort of inconsistency in systems of classification based largely on spore characters and mature conditions of ascocarps. However, one cannot make very great changes based on the comparatively few and often fragmentary and uncertain researches that have been made. For example, the lichens must be interpolated, for the present, in large groups among other ascomycetes, though they may need further distribution after we know more about life histories. The general similarity of the reproductive tracts in a large majority of the lichens that have been studied, the resemblance of the somatic tracts in large groups of lichens, and the rather limited knowledge of the relationship between lichens and other ascomycetes justify this conservatism in distribution.

In previous arrangements of ascomycetes in a single system, no discussion of possible or probable homologies and relationships has been attempted. With our present limited knowledge, such discussion must serve as an argument for the method rather than a very great help in the arrangement. Unfortunately, we must continue to base our taxonomic treatment of ascomycetes quite largely on spore characters and on the structure of mature fruits until we have sufficient data to enable us to use more fundamental characters. However, in the plan of classification to follow, the *Lecanorales* have been kept distinct from the *Pezizales,* partly because the lichens that have been examined from the former group have, on the whole, a similar type of reproductive organs, more complicated than those in the latter group, in which these tracts are as a whole more degenerate, or possibly more primitive. Which of these two orders should stand higher is still an open question, regarding which certain statements are made below. For the present, we have placed the order which has the more specialized somatic structure higher. However, it is readily admitted that the higher form of vegetative structure may indicate either less of degeneration or a better development because of the advantageous conditions under which the lichens live. Again, if the *Ascomycetac* have arisen from the *Rhodophyceae,* a consideration to be taken up below, the *Lecanorales* may yet be proved to have, as a whole, a shorter line of descent than the *Pezizales.*

Whatever consideration we may give to somatic characters and carpologic structure as a basis for classification, it seems certain that the character of reproductive tracts forms a more valuable criterion. Yet it needs to be kept in mind that sometimes, as in the *Collemaceae*, forms which differ greatly with respect to structure of sexual organs and sexual behavior are so much alike with respect to vegetative characters and mature carpologic structure that the latter features have had greater weight in taxonomic disposition. The plant studied by Miss Bachman (1 and 2) illustrates well the point suggested above. It is probably more primitive than members of the *Collemaceae* whose sexual reproductive areas show spermatia in spermagonia, the evolution of the male reproductive area having probably lagged while carpologic structure and somatic conditions advanced in the direction followed in the evolution of the genus *Collema*. In spite of the rather striking resemblance of the reproductive areas of the so-called *Collema pulposum* studied by Miss Bachman and those of *Ascobolus carbonarius* examined by Dodge (23), one cannot overlook somatic characters to the extent of placing the former plant with the *Ascobolaceae* rather than with the *Collemaceae*. This is one striking instance in which vegetative characters and carpologic structure have great value in classification; but it is scarcely possible that plants which have such different male reproductive areas as Miss Bachman's plant and the one examined by Stahl (59) (Fig. 5) should both be assigned to the same species, *Collema pulposum*.

Studies of certain ascomycetes show that forms which differ greatly with respect to somatic and carpologic structure and therefore are far removed from each other in present systems of classification have very similar reproductive areas, while others much alike with respect to somatic and carpologic structure, but very different in regard to male or female reproductive areas or both, have been placed in the same family, the same genus, or even in the same species. For instance, the genus *Ascobolus* shows a wide range of variation with respect to sexual areas, while the range is much wider for the *Ascobolaceae* as a whole. A full discussion of conditions found in this family may be found in one of the papers cited from Dodge (23). While the student who deals with ascomycetes from the taxonomic point of view must endeavor to familiarize himself with all studies of the life histories of these fungi, it is by no means clear at present just what changes should be made in existing systems of classification on account of the facts more or less clearly, fully, and certainly ascertained regarding reproductive processes and ontogeny. At least, a good deal of conservatism may well be observed until our information is greatly increased so that many facts which have a bearing on classification may be known and considered in correlation.

Our knowledge of the development of the ascocarp is perhaps even more fragmentary than that of the sexual apparatus, toward which a large portion of the recent work has been directed. It is still an open question whether the cleistothecium, the perithecium, or the apothecium is the most primitive form of the ascocarp; and the whole development of many carpologic structures in various groups of ascomycetes must be carefully studied before we may know their worth as criteria for constructing a system of classification.

The Besseys (8 and 9) think that there is good reason to believe that *Collema*-like plants with apothecia, like the one studied by Miss Bachman, may be the most primitive of existing *Ascomycetae* and closely related to the *Rhodophyceae*. This suggestion seems reasonable since the species of *Collema* and Miss Bachman's plant are low forms of lichens vegetatively, the thalli being mycelia devoid of plectenchymatous structure, while the plants are apparently near relatives of such families as the *Lecideaceae*, the *Gyalectaceae*, and the *Ascobolaceae*, all of which may be rather primitive ascomycetes. Of these groups, Miss Bachman's plant and *Ascobolus carbonarius*, studied by Dodge, are nearest the *Rhodophyceae* of those that have been examined with respect to reproductive tracts, and may well be regarded as the most primitive ascomycetes whose life histories have been investigated. Of the two plants, Miss Bachman's, on account of the character of its male reproductive organs, appears to be nearer the *Rhodophyceae*. Yet the view that the first ascomycetes were algicolous is opposed to the one commonly held by botanists to the effect that lichens may be traced back to non-algicolous ascomycetes. If the theory that the most primitive ascomycetes are those having apothecia be true, of course much more investigation is needed before we can safely decide whether the primitive forms were lichen or non-lichen. If lichen, it may be that we have the most primitive of existing forms among such members of the *Collemaceae* as possess the low vegetative structure noticed above and reproductive tracts and sexual behavior most like those known in the *Rhodophyceae*. The primitive forms are probably to be sought among those that live in loose relationship with the algal host, but are still largely dependent on this host. The *Collemaceae* fulfill these conditions, since they do not, with one or two exceptions, form haustoria, but simply penetrate throughout the gelatinous *Nostoc* colonies, confining their course to the sheaths and scarcely injuring the protoplasts, while they are but weakly attached to the substratum by rhizoids and are almost wholly dependent on the host for nourishment. From such a primitive form of ascomycete, there could be two lines of descent, one of which would give rise to higher lichens with foliose and fruticose thalli, close relationship with the algal host, and the apothecial form of ascocarp retained, while the other would produce the lower lichens which are crustose upon the substratum or sunken into it and which live in increasingly loose relations with the algal host as they sink into the substratum. Some of these forms could have lost the algal habit gradually as they came into closer and closer relationship with the substratum and so have given rise to non-algicolous ascomycetes. As a rule, lichens which have perithecia or hysterothecia are those that are sunken into the substratum, while those that are crustose upon the surface, or are foliose or fruticose, usually have apothecia. On the theory that the apothecium is the primitive form of ascocarp, perithecia and hysterothecia would arise as protective structures in reaction to xerophytic habit or sinking into the substratum. Of course we may begin with such a form as *Ascobolus carbonarius*, suppose that it evolved a form having the algicolous habit, and then apply the above reasoning equally well. Therefore, the rather unimportant question whether primitive ascomycetes were lichens or not, is not so easy to settle, though it is reasonable to suppose that certain *Rhodophyceae* which had become parasitic on other marine algæ may have acquired a terrestrial habit, passed into parasitic relationship with terrestrial algæ, and acquired the ascomycetous forms of reproduction and carpologic structure as a response to changed conditions of environment. The relation of the lichen to its algal host and to the substratum touches this problem and is discussed in a previous paper (Fink 31).

To generalize from finding one or two plants which have apothecia and at the same time possess reproductive areas and processes much like those found in the *Rhodophyceae* would be a very uncertain procedure; but the discussion by Dodge (24) shows plainly that the generally favored theory that the perithecium is the primitive form of the ascocarp rests on very uncertain evidence at best. While it is certain that many careful studies of carpologic structure and development will be necessary before we may know with any reasonable degree of certainty whether the apothecium or the perithecium is more primitive, it has seemed reasonable, in view of all the evidence at hand, to adopt a sequence of orders of ascomycetes which comports in a general way with the view that the apothecium is the primitive form of ascocarp. In following this view, it has seemed best to place the algicolous discomycetes above the non-algicolous forms because of their higher somatic development and the general resemblance between their sexual reproductive tracts and those of the pyrenomycetes above them. In so doing, it is plainly seen that any method that could be followed is open to criticism and liable to be proved incorrect by further research.

The resemblances between the sex organs of the *Ascomycetae* and the *Rhodophyceae* have been a matter of repeated discussion since the time of Stahl's work on the *Collemaceae* and have been greatly emphasized since by the researches of Thaxter (61), Bachman (1 and 2), Dodge(24), and others. The ascogenous hyphae of the *Ascomycetae* likewise have been homologized with the ooblastema filaments of the *Rhodophyceae,* while a relationship has been suggested between asci and the gonidioblasts which arise as the result of secondary fusions among the red algæ. If the evident parallelism in development among the *Ascomycetae* and the *Rhodophyceae* rests on supposed homologies, we may also conclude that ascocarps and cystocarps are homologous structures, and that the former group arose from the latter, or that the two groups had at least a common origin. One of the two suppositions just stated must be adopted, or we must follow those who think that these parallelisms do not rest upon homology. This matter is fully treated by Dodge (24).

In this connection, it might prove worth while to reëxamine the forms of parasitism found among the *Rhodophyceae,* and reproductive and somatic tracts in these parasitic algae, with a special view of attempting to shed some light on the problem of possible affinities between the *Rhodophyceae* and the *Ascomycetae.* It is even possible that, if ascocarps are to be homologized with glomerules and cystocarps, and much more fundamental and significant homologies exist between structures which lead up to these mature fruits, such studies would indicate a multiple origin of the *Ascomycetae* from the *Rhodophyceae* and suggest that more than one type of ascocarp may be primitive. Such studies might also help to decide whether forms of ascomycetes which have similar ascocarps are all closely related, or whether certain groups which have very different ascocarps are not sometimes nearly related.

Whatever the future may prove regarding the various possible or probable homologies between the *Ascomycetae* and the *Rhodophyceae,* it is certain that the theory of the origin of the former from the latter is the most plausible one that has been offered regarding the phylogeny of all undoubted ascomycetes, algicolous and non-algicolous.

Cytological studies must prove increasingly valuable in our studies of the relationships among ascomycetes. Especially will knowledge of nuclear behavior in the reproductive tracts finally have considerable weight in the arrangement of ascomycetes, since it will enable us to decide just what portion of an archicarp is the ascogonium. At present nuclear behavior is not known in the sexual reproductive tracts of any lichens save one (Bachman 2), nor is it well understood in many other ascomycetes. According to Claussen (16), delayed nuclear fusions and homologous alternation in ascomycetes strongly resemble the conditions found in certain basidiomycetes. This points to the origin of the latter group from the former, and further studies of nuclear behavior in both groups may shed some light on the relative rank of the various ascomycetes. The rather uniform character of ascogenous hyphae and the peculiar origin of asci from them, together with the characteristic behavior of the nuclei within these structures, is probably the strongest proof of the common, or at least similar, ancestry of all ascomycetes.

There is another theory of the origin of ascomycetes that must be noted. Bucholtz (15) has presented a modification of the theory of origin of the *Ascomycetae* from the *Phycomycetae* which is especially worthy of consideration. He considers *Endogone* to be a plant whose fruit results from the conjugation of heterogametes. After cytoplasmic fusion, the two nuclei pass together from the oogonium into a protrusion, which might be regarded as a primitive ascus. Here the nuclei fuse. Not far removed from this is the formation of asci as direct outgrowths from the single fertilized ascogenic cell described by Faull (26) for *Amorphomyces* and said to occur in some other genera of the *Laboulbeniales*. Nienburg (51), Claussen (16), and others have also presented strong arguments for this theory, which would make trichogynes and ascogenous hyphæ structures which arose independently in ascomycetes, would deny the origin of the *Ascomycetae* from the *Rhodophyceae,* and would account for the resemblances between these two groups by parallelism alone. However, the evidences of relationship between the two groups are too strong to be offset by such facts as have been advanced hitherto for the origin of the *Ascomycetae* from the *Phycomycetae.*

It will be seen from the above presentation that no attempt has been made to consider the problem of classification of ascomycetes merely as it applies to our studies in Ohio. The outline of classification that is presented herewith is the result of a study of the problem concerned with the phylogeny of all ascomycetes. To base any system of treatment, even for a small area, on anything less than a consideration of all ascomycetes as to their origin and relationships would be to invite serious failure. Consequently, in preparing the system to follow, all the orders of ascomycetes have been considered, while many families that do not occur in our flora, and, consequently, do not appear in the outline, have been kept in mind, and have been discussed in part. How these families should be treated will be taken up more fully in the third paper of the series on "The nature and classification of lichens" (Fink 30 and 31), in which the whole problem of the classification of ascomycetes will be reconsidered with such additional data as may come to light in the interval.

As stated in the introductory paragraph of this paper, ascomycetes have been treated previously as a whole. Lists from Nebraska (Webber 64 and 65) and California (McClatchie 46) have distributed lichens among other ascomycetes, and certain writers (Bessey 6, 7 and 8; Clements 17 and 18; Fink 28, 29 and 31, and Schaffner 54) have either united all ascomycetes into one system or intimated that this method of treatment is in accord with present knowledge of the group. Certain European mycologists regard lichens as fungi, and some of them have either advocated their distribution among other fungi, or have admitted that they may, without inconsistency, be so treated (Fink 31). The disposition proposed below is based on the belief that we have sufficient data, in part briefly outlined above, to warrant the distribution of lichens in the best manner possible in order that we may present relationships better and have a good basis for comparative studies of all ascomycetes. The statement in this paragraph expresses views that are held by various botanists and have been used in certain arguments, keys, catalogues of plants, and systems of classification cited. However, this series of papers will be the first to treat lichens as fungi with other ascomycetes in a descriptive catalogue.

A summary regarding the arrangement of the orders and some of the families will elucidate some points. The *Hemiascales* (*Hemiascineae*) of some authors have not been admitted, though *Eremascus* and some others of these plants may yet prove to be ascomycetes rather than phycomycetes. The *Laboulbeniales* have been placed first in the outline of classification, since the work of Thaxter (6) and Faull (26 and 27) makes them undoubted though aberrant ascomycetes, apparently near to the *Rhodophyceae*, which have similar archicarpic characters. With respect to ascogenous structures, they must be regarded either degenerate or closely related to those members of the *Rhodophyceae* that produce ooblastema filaments, while the closed ascocarp would seem to indicate higher rank than is given to the order. In any event there seems to be no good place to interpolate the *Laboulbeniales* among the other orders, and first place appears to accord better with present knowledge than the place at the end of the ascomycete series to which the order has been assigned more commonly. In placing the order first, one could not afford to commit himself to the belief that the *Laboulbeniales* are nearer to the *Rhodophyceae* than are the *Pezizales* and the *Lecanorales,* which in turn are probably more plainly related to the orders that follow in the outline. The two orders just named are placed second and third in the series on the theory, based on carpologic development and structure, that they, too, are closely related to the *Rhodophyceae.* The *Lecanorales* have been kept in one large group rather than split up into two or more orders, partly on account of their close relationship among themselves and partly because further study may result in a more or less radical rearrangement, which is likely to involve the *Pezizales* as well. For instance, the *Collemaceae,* the *Gyalectaceae,* and the *Lecanactidaceae* seem to be, partly in light of studies reviewed above, nearer to some of the *Pezizales* than we are able to indicate in our scheme of classification. Some students of ascomycetes favor separating the inoperculate members of the *Helvellales* from those that are operculate. If this be done, the group may well be distributed among the *Pezizales.* The order *Helvellales* has been retained for the present and is placed near the *Pezizales,* to which it seems to be closely related. The *Tuberales,* which have been variously treated by students, seem to be near relatives of both the *Pezizales* and the *Helvellales,* the peridium being probably a reaction to subterranean position of the ascocarp. Interpolation of the *Lecanorales* prevents placing the *Helvellales* and the *Tuberales* in succession immediately after the *Pezizales,* but this is only one of the many unavoidable difficulties met in efforts to formulate schemes of classification which will bring together forms that seem to be closely related. Proper sequence of the families of the *Pezizales* depends on whether the simpler archicarps are primitive or degenerate, a point not fully determined. Consequently, the families are arranged in an order which leads up to the *Lecanorales,* which are placed next above. This arrangement shows the relationship between the two orders by passing from strictly nonalgicolous to partially algicolous families of the *Pezizales,* thence to the algicolous *Lecanorales.* Of course this method must eventually give way, if need be, to better knowledge of the reproductive areas and related development. Since the *Lecanorales* in general show great similarity in sexual reproductive areas, the sequence of families is based on apothecial and vegetative structure, though it is plainly seen that increasing knowledge of degeneration in the sexual areas and the sexual processes may soon require some modification of this method. Regarding the *Phacidiales* and the *Hysteriales,* it is quite possible that further study may result in placing some of the lichens in the former order, nor is it certain that these orders are intermediate between discomycetes and pyrenomycetes. Concerning the angiocarpic groups, it is not probable that the perithecia and the cleistothecia all arose in similar manner, or that they are so closely related as the order adopted would indicate. The *Pyrenulales* are placed after the non-algicòlous groups for about the same reason that the *Lecanorales* are placed after the *Pezizales.* Here again, further studies are likely to require some modification of the method used herein. The *Perisporiales,* the *Aspergillales,* the *Exoascales,* and the *Saccharomycetales* have been placed toward the close of the series since, if the theory of origin of the *Ascomycetae* from the *Rhodophyceae* be true, each of these orders, as a whole, seems to be composed of either degenerate or doubtful ascomycetes. Degeneration seems probable, on this basis of origin, in the simple reproductive tracts tending toward likeness in form and size of gametes, in reduction and final loss of the trichogynes, and in undoubted isogamy in a few instances among the saccharomycetes, though in this order the conjugation, rarely observed, may be a secondarily acquired character.

In closing, it should be stated that all speculations regarding the relationships of ascomycetes are rendered more uncertain by the probability that carpologic evolution may have proceeded in nearly parallel lines in various groups so that forms that differ considerably with respect to archicarps and ascocarps may be more closely related than others that show considerable similarity with respect to these areas.

In the studies of the orders and families of Ohio ascomycetes to follow in this series of papers, the better-known groups will be published while field work and laboratory investigations are increasing our knowledge of orders at present unknown to our flora, or poorly understood. The system of classification proposed herein will serve as a basis for the work and will indicate where each group studied is related in our scheme of classification adopted for the ascomycetes as a whole. The final work on the ascomycetes of Ohio should be to bring these studies together under a system of classification revised sufficiently to show the advance in knowledge of the group while the preliminary studies are in progress. The provisional arrangement which is to serve as a basis for the study of various groups of Ohio ascomycetes is given below.

CLASS ASCOMYCETAE

I. LABOULBENIALES (LABOULBENIINEAE)

Many species of this order doubtless are present in Ohio, though none have been listed.

II. PEZIZALES (PEZIZINEAE)

1. PYRONEMACEAE. The genus *Pyronema* is known in Ohio.
2. PEZIZACEAE. Genera known in Ohio are *Peziza, Lachnea. Geopyxis, Humaria, Otidea,* and *Urnula.*
3. ASCOBOLACEAE. Genera known in Ohio are *Ascobolus, Lasiobolus, Ascophanus, Saccobolus,* and *Rhyparobius.*
4. HELOTIACEAE. Genera known in Ohio are *Helotium, Sarcoscypha, Chlorosplenium, Ciboria, Sclerotinia, Arachnopeziza, Dasycypha, Stamnaria, Ombrophila, Coryne,* and *Phialea. Sclerotinia tuberosa* sometimes grows with an alga.
5. MOLLISIACEAE. Genera known in Ohio are *Mollisia, Tapesia, Orbilia, Belonidium,* and *Pezizella.*
6. CENANGIACEAE. Genera known in Ohio are *Cenangium, Cenangella, Dermatea, Tympanis, Sarcosoma,* and *Holwaya.* There are some primitive lichens in this family.
7. PATELLARIACEAE. Genera known in Ohio are *Patellaria, Patellea, Patinella, Karschia, Leciographa, Durella,* and *Biatorella.* Certain species of *Patellea, Patinella, Karschia, Leciographa,* and *Biatorella* are lichens.

III. LECANORALES (LECANORINEAE)

1. LECANACTIDACEAE. The genus *Lecanactis* is known in Ohio.
2. LECIDEACEAE. Genera known in Ohio are *Lecidea* including *Biatora*), *Bacidia, Lopadium, Buellia, Psora, Toninia,* and *Rhizocarpon.*
3. CLADONIACEAE. The genus *Cladonia* is known in Ohio.
4. COLLEMACEAE. Genera known in Ohio are *Collema, Synechoblastus, Leptogium,* and *Mallotium.*

5. PANNARIACEAE. Genera known in Ohio are *Pannaria, Heppia,* and *Placynthium.*
6. STICTACEAE. Genera found in Ohio are *Sticta* and *Lobaria.*
7. PELTIGERACEAE. Genera known in Ohio are *Peltigera, Peltidea,* and *Nephroma.*
8. ACAROSPORACEAE. The genus *Acarospora* is known in Ohio.
9. LECANORACEAE. Genera known in Ohio are *Lecanora* and *Ochrolechia.*
10. PERTUSARIACEAE. The genus *Pertusaria* is known in Ohio.
11. PARMELIACEAE. Genera known in Ohio are *Parmelia, Anzia, Cetraria,* and *Nephromopsis.*
12. USNEACEAE. Genera known in Ohio are *Usnea, Ramalina, Alectoria,* and *Evernia.*
13. TELOSCHISTACEAE. Genera known in Ohio are *Teloschistes, Placodium* (*Calopisma*), and *Xanthoria.*
14. PHYSCIACEAE. Genera known in Ohio are *Physcia, Pyxine, Anaptychia,* and *Rinodina.*
15. GYROPHORACEAE. Genera known in Ohio are *Gyrophora* and *Umbilicaria.*

IV. CALICIALES (CALICIINEAE)

1. CALICIACEAE. Genera known in Ohio are *Calcium, Chaenotheca, Stenocybe,* and *Cyphelium.* These plants are mostly lichens.

V. HELVELLALES (HELVELLINEAE)

1. GEOGLOSSACEAE. The genus *Leotia* is known in Ohio.
2. HELVELLACEAE. Genera known in Ohio are *Helvella, Morchella,* and *Gyromitra.*

VI. TUBERALES (TUBERINEAE)

No members of this order have been reported from Ohio.

VII. PHACIDIALES (PHACIDIINEAE)

1. STICTIDIACEAE. Genera known in Ohio are *Stictis, Propolis, Mellittiosporium, Schizoxylon,* and *Lichenopsis.*

2. TRYBLIDIACEAE. Genera known in Ohio are *Tryblidium* and *Scleroderris.*

3. PHACIDIACEAE. Genera known in Ohio are *Phacidium, Coccomyces,* and *Rhytisma.*

VIII. HYSTERIALES (HYSTERIINEAE)

1. HYPODERMATACEAE. Genera known in Ohio are *Angelinia* and *Lophodermium.*

2. DICHAENACEAE. The genus *Dichaena* is known in Ohio. Some of the species may be lichens.

3. HYSTERIACEAE. Genera known in Ohio are *Hysterium, Hysterographium,* and *Glonium.*

4. ACROSPERMACEAE. The genus *Acrospermum* is known in Ohio.

5. GRAPHIDACEAE. Genera known in Ohio are *Graphis* and *Opegrapha.*

6. ARTHONIACEAE. Genera known in Ohio are *Arthonia* and *Arthothelium.*

IX. HYPOCREALES (part of the PRYENOMYCETINEAE)

1. HYPOCREACEAE. Genera known in Ohio are *Hypocrea, Hypocrella, Hypocreopsis, Hypomyces, Melanospora, Letendraea, Nectria, Pleonectria, Ophionectria, Cordyceps, Claviceps, Typhodium,* and *Gibberella.*

X. DOTHIDIALES (part of the PYRENOMYCETINEAE)

1. DOTHIDIACEAE. Genera known in Ohio are *Dothidea, Phyllachora,* and *Plowrightia.*

XI. SPHAERIALES (part of the PYRENOMYCETINEAE)

1. CHAETOMIACEAE. The genus *Chaetomium* is known in Ohio.

2. SORDARIACEAE. Genera known in Ohio are *Sordaria* and *Sporormia.*

3. SPHAERIACEAE. Genera known in Ohio are *Sphaeria, Lasiosphaeria, Trichosphaeria, Herpotrichia, Bombardia, Acanthostigma, Rosellinia, Bertia,* and *Zignoella.*

4. CERATOSTOMACEAE. Genera known in Ohio are *Ceratostoma* and *Ophioceras.*
5. CUCURBITARIACEAE. Genera known in Ohio are *Cucurbitaria, Nitschkia,* and *Coelosphaeria.*
6. AMPHISPHAERIACEAE. Genera known in Ohio are *Ohleria, Trematosphaeria,* and *Caryospora.*
7. MYCOSPHAERELLACEAE. Genera known in Ohio are *Mycosphaerella* and *Guignardia.*
8. PLEOSPORACEAE. Genera known in Ohio are *Pleospora, Venturia, Didymella, Leptospraeria, Ophiobolus,* and *Pyrenophora.*
9. GNOMONIACEAE. Genera known in Ohio are *Gnomonia, Gnomoniella,* and *Phomatospora.*
10. VALSACEAE. Genera known in Ohio are *Valsa, Anthostoma, Kalmusia, Diaporthe, Eutypa,* and *Eutypella.*
11. MELANCHONIDACEAE. Genera known in Ohio are *Valsaria, Calospora,* and *Pseudovalsa.*
12. DIATRYPACEAE. Genera known in Ohio are *Diatrype, Diatrypella,* and *Quaternaria.*
13. MELOGRAMMATACEAE. The genus *Botryosphaeria* is known in Ohio.
14. XYLARIACEAE. Genera known in Ohio are *Xylaria, Nummularia, Ustulina, Hypoxylon, Daldinia,* and *Poronia.*

XII. PYRENULALES (PYRENULINEAE)

1. VERRUCARIACEAE. Genera known in Ohio are *Verrucaria* and *Staurothele.*
2. PYRENULACEAE. Genera known in Ohio are *Pyrenula, Arthopyrenia,* and *Leptorhaphis.*
3. DERMATOCARPACEAE. Genera known in Ohio are *Dermatocarpon* and *Endocarpon.*
4. TRYPETHELIACEAE. The genus *Trypethelium* is known in Ohio.
5. MYCOPORACEAE. The genus *Mycoporum* is known in Ohio.

XIII. PERISPORIALES (part of the PYRENOMYCETINEAE)

1. Erysibaceae. Genera known in Ohio are *Erysibe, Sphaerotheca, Podosphaera, Microsphaera, Uncinula,* and *Phyllactinia.*

2. Perisporiaceae. Genera known in Ohio are *Dimerosporium, Scorias, Antennaria,* and *Apiosporium.*

3. Microthyriaceae. The genus *Asterina* is known in Ohio.

XIV. ASPERGILLALES (ASPERGILLINEAE)

1. Gymnoascaceae. The genus *Gymnoascus* must occur in Ohio.

2. Aspergillaceae. Genera known in Ohio are *Aspergillus* and *Penicillium.*

XV. EXOASCALES (EXOASCINEAE)

1. Exoascaceae. Genera known in Ohio are *Exoascus* and *Taphria.*

XVI. SACCHAROMYCETALES (SACCHAROYMCETINEAE)

1. Saccharomycetaceae. The genus *Saccharomyces* is known in Ohio.

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EXPLANATION OF PLATES I AND II

The figures are intended primarily to illustrate some types of female reproductive tracts in ascomycetes. The magnification is given wherever this datum was available.

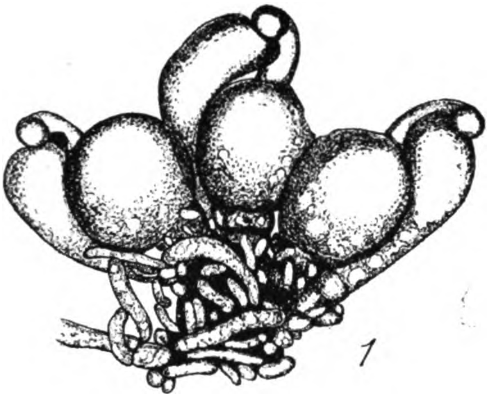
PLATE I

Fig. 1. Three archicarps of *Pyronema confluens* with spheroidal, one-celled ascogonia surmounted by one-celled trichogynes. Each trichogyne tip is in contact with an antheridium. From Harper.

Fig. 2. A transverse section of an archicarp of *Lachnea stercorea.* The one-celled ascogonium is at the left and passes into the several-celled trichogyne, which extends to an antheridium at the right above. x 600. From Miss Fraser.

Fig. 3. A section of a leaf showing the coiled archicarp of *Polystigma rubrum* and the vegetative hyphae which pass through the stoma. x. 900. From Blackman and Welsford. See also the discussion of Nienburg's results on this plant.

Fig. 4. A reconstruction from sections of *Laboulbenia chaetophora* to show the complete outer wall of the perithecium, one cell of the inner wall, the enclosed ascogonium surmounted by the trichophoric cell, and the terminal, branched trichogyne. x 450. From Faull.



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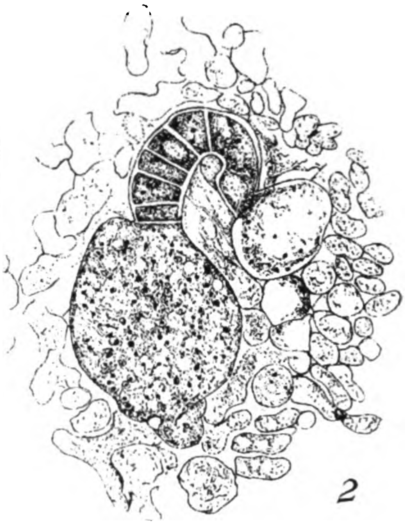

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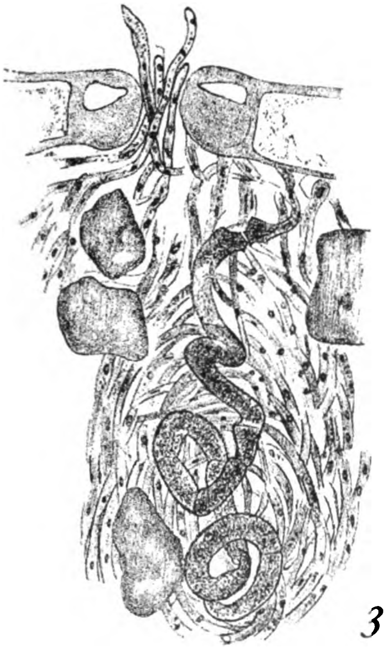

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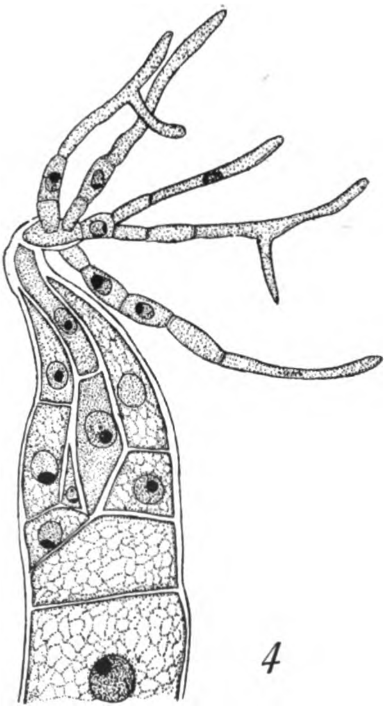

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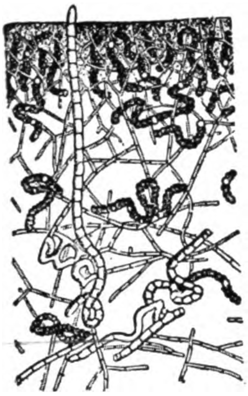
PLATE II.

Fig. 5. The many-celled archicarp of *Collema microphyllum.* The coiled ascogonium passes into the erect trichogyne, which in turn extends above the surface of the algal-host colony. x 300. From Stahl.

Fig. 6. The many-celled archicarp of Miss Bachman's *Collema*-like plant. The coiled ascogonium is at the left, and the trichogyne extends to a group of internal spermatia (antheridia?) at the right. x 520. From Miss Bachman.

Fig. 7. A mature archicarp *of Ascobolus carbonarius*: a, a conidium which gives rise to an archicarp; b, the conidiophore; d to g, the stalk of the archicarp; g to j, the ascogonial coil; h, probably the ascogonium proper; k to m, the trichogyne; m, the antheridial conidum; n, the conidiophore. x 400. From Dodge.

Fig. 8. The archicarp of *Peltigera canina.* One of four cells of the ascogonium is shown at A, and a cell of the vegetative hypha from which the archicarp arose is shown at s. There is supposed to be no trichogyne. x 750. From Fünfstück.



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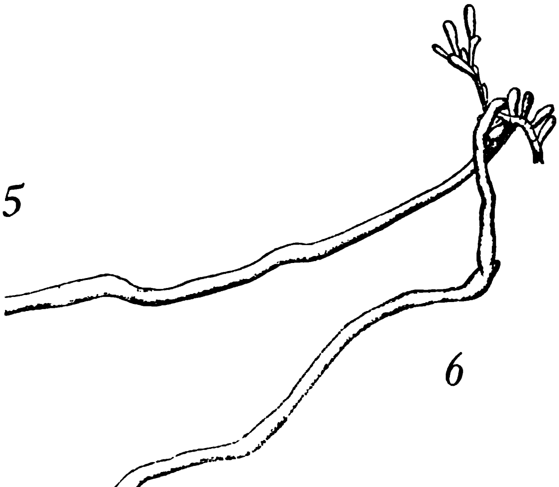

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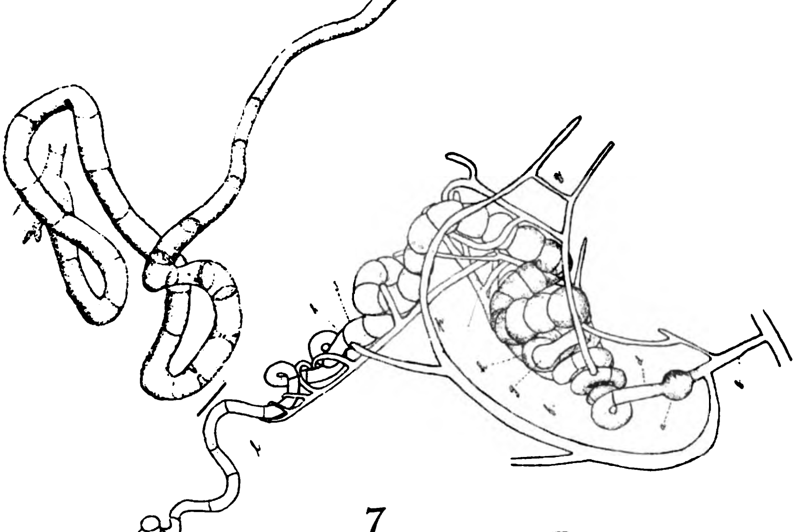

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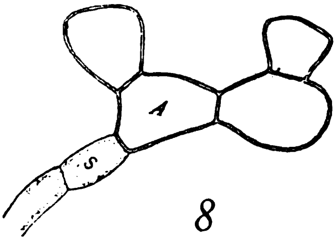

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Bruce Fink.

THE ASCOMYCETES OF OHIO.—II

The Collemaceae*

BRUCE FINK AND C. AUDREY RICHARDS

General Considerations

Hitherto comparatively few descriptions of lichens as fungi have been undertaken. In many short diagnoses of lichens, mention of the algal hosts has been omitted, and many lichens have been treated thus inadvertently as fungi. But in more lengthy diagnoses or descriptions, the common practice has been to consider the algal host as part of the lichen. In order to dispose of typical lichens as fungi, no greater departure from the ordinary methods is required than to omit from the descriptions all reference to the algal host, the thing which is now often done through inadvertency. However, in order to apply to a few families of lichens the methods commonly employed in the taxonomic disposition of fungi, a method must be followed which diverges considerably from that which has been employed by lichenists.

If it should be found impracticable to treat any group of ascomycetous lichens as fungi, the whole plan of treatment of ascomycetes proposed in the first paper of this series would be impossible of execution. Consequently, we have considered, in this second contribution toward a knowledge of the ascomycetes of Ohio, a family of lichens, the treatment of which as fungi probably involves as wide a departure from the method commonly employed by students of lichens as any group that could be chosen. In order to demonstrate as early as possible in this series of papers how slight are the changes required in order to treat the large majority of lichens as fungi, the *Lecideaceae,* another family of lichens, will receive consideration in the next paper of this series.

The study of the *Collemaceae* has been made classic through the contributions of several botanists. De Bary studied this group and ascertained that the chlorophyllous cells are algal (3). Schwendener soon extended this view to include the chlorophyllous cells found in all lichens (6). Stahl chose members of the same family for the first important work on sexual reproduction in lichens (7). Sturgis (8) and Baur (4) have since confirmed Stahl's results. Miss Bachman (1 and 2) has found in a member of the *Collemaceae* an interesting condition with respect to the morphology and the behavior of the sexual reproductive tracts and has obtained in the same plant the only important cytological results thus far secured in the study of the sexual organs of lichens. The results obtained by these workers are known to many botanists, have been considered in part in the first paper of this series, and need no further discussion here.

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* Contributions from the Botanical Laboratory of Miami University—XII.

In working out a new taxonomic method, there is a distinct advantage in considering a group of plants in which many botanists are interested. However, our prime motive in selecting the *Collemaceae* was, as explained above, to attack first a family of lichens, the treatment of which as fungi probably presents as many difficulties as any that could be selected. The species of this family grow mainly within the algal hosts instead of containing these hosts in a limited area within somatic tracts of the parasites as do the great majority of lichens; and the descriptions of gross characters hitherto given as morphological features of members of the *Collemaceae* belong largely to the algal hosts rather than to the lichens themselves. Finding a satisfactory way to obviate this difficulty and devising a new method for the study of the minute morphology of these lichens have required spending much time and energy on details, some of which have proved to be of little if any taxonomic value and have not been included in the results presented in this paper. One year was given to working out a method, which, in the last two years, has been further elaborated in the studies of the *Collemaceae* of Ohio presented herein.

In connection with many difficulties encountered, it is fortunate that the tissues of members of the *Collemaceae* appear more distinctly in sections than do those of the majority of lichens. This condition has made it comparatively easy to study most of the details with respect to structure of cortices, medullæ, sexual reproductive tracts, and apothecia. In a few instances, we have resorted to imbedding and serial sectioning; but most of our results have been obtained by free-hand sectioning with the razor. Flemming's triple stain, Delafield's hæmatoxylin, and safranin were used with good results; but we depended mainly on the solution of iodine which is used commonly in the study of lichens. Other reagents used were water, potassium hydrate, Schulze's macerating fluid, and alcohol. For macerating, potassium hydrate was found more satisfactory than Schulze's solution. The measurements of microscopic features were taken from specimens treated with water only.

Limiting the area studied to a region near at hand gave the advantage of being able to secure material in fresh condition easily. While our area conforms to the requirements of the Ohio Biological Survey, the collecting has been confined to the southwestern portion of the state, extending roughly about one-fourth of the distance from the southern boundary to the northern and somewhat more than one-third of the way from the western boundary to the eastern. The principal collecting grounds are about Oxford, Eaton, West Alexandria, Mason, Washington Court House, Greenfield, Paint, Bainbridge, Peebles, and Cincinnati. Collections made by others in various portions of the state have been studied through material loaned from the herbarium of the Ohio State University and have given a fairly satisfactory knowledge of the distribution of several of the species within the state as a whole.

Just what changes in limitations of species would result from the employment of a new taxonomic method could not be known until we had examined a considerable number of species of the family. While our paper covers only the sixteen species of the *Collemaceae* known in Ohio, we have made preliminary examinations of about as many more. This means that we have covered approximately one-fourth of the species known to occur in North America. Thus far our method has not required any changes in species-limits. Each species studied has shown a sufficient number of morphological characters to mark it as distinct, or has been found to modify the size, form, color, or general appearance of the algal host in a peculiar manner. In our descriptions, the power of modifying the algal-host colony has been treated as a specific, physiological character of each species of lichen. Since the algal host rather than any portion of the lichen itself, except the apothecia, is conspicuously visible in the field, we have given first under each name of a species a statement concerning the manner in which the lichen has modified its host. This brings into prominence that which is seen plainly on first observation, and at the same time avoids the error of describing the algal host as a portion of the lichen. Following the statement regarding the transforming action of the lichen on the algal host, such characters of the lichen itself as have seemed to have considerable diagnostic value have been recorded.

We have tried to present a method workable for the species found in the area treated in this paper and also like that which must be employed when our method is extended to include the *Collemaceae* of a larger area, or finally to the family as a whole. It is evident that the taxonomic value of the diagnostic characters used, both morphological and physiological, may be better known after a large number of species has been studied carefully, but it is not probable that extension of the method given herein will involve other than minor modifications.

In deciding on a method of treatment of the algal host, other ascomycetous lichens which will require treatment similar to that which is given to the *Collemaceae* in this paper were kept in mind. Other nosticolous lichens may be treated in essentially the same manner as the *Collemaceae*. Other types are illustrated by *Ephebe*, the thallus of which is similar to that of the *Collemaceæ*, but is found penetrating throughout the tissue of the branched, filamentous alga, *Sirosiphon*, and by *Coenogonium*, which has a mycelial thallus that covers a portion of the filaments of the algal host, *Trentepohlia*. From a purely technical point of view, it would be better, in treating the *Collemaceae* and all other lichens which require special methods for disposition of the modified algal host, to treat the host in a paragraph following the description and dealing with habitat and distribution. However, the practical advantage of placing immediately under the name of the species that which is first noticed in field or laboratory is so great that all who use our descriptions will doubtless agree that we are justified in departing from a more exact scientific procedure sufficiently to place the statement about the transformation of the algal host before the description of the lichen, which, excepting its apothecia, is known only through microscopic study.

The penetration of the thallus of members of the *Collemaceae* throughout the algal-host colony as a distinct mycelial structure unattached to the algal cells (Fig. 1) renders the somatic areas so plainly visible that even the sexual reproductive areas, imbedded in the vegetative structures, are much more readily visible in section than those of most other lichens. In beginning our work, it was thought that these reproductive structures, so plainly visible, might be available in this family of lichens for diagnostic purposes. The archicarps (Fig. 18) and the spermagonia (Fig. 25) were carefully described for each species of *Synechoblastus* studied, and later those of a majority of the species of our other genera were more or less carefully examined, even though the work on *Synechoblastus* indicated that these organs do not differ enough in the various species examined to make them of diagnostic value, except in a few instances. Added to this is the difficulty, sometimes very great, of finding specimens that bear the sex organs, and the areas of the thallus in which these organs occur.

The sex organs grow, for most part, during two months in the spring and for the same length of time in autumn. These organs may be found in specimens not collected during these periods; but the cells are likely to be dead, and the parts of the archicarps collected out of season are not likely to have quite their natural form. The spermagonia likewise must be studied at the right time, since the spermatia decrease in numbers and finally disappear entirely after the prime condition is past, while the basidia become considerably enlarged. The spermagonia usually appear as minute protuberances, which are commonly some shade of yellow or brown. They occur most frequently on the lobes and near the margins, or at least externally to the areas occupied by mature apothecia. They may be seen easily with a hand lens, especially after the lichen and the algal host are moistened; but they are not easily distinguished, in gross morphology, from young apothecia, which have not yet ruptured the mass of structures which lie above them. There is no way of detecting the presence of archicarps through external appearance, but they usually occur toward the margins from the position occupied by the scattered apothecia. Sometimes, however, the archicarps are found within the region of the thallus occupied by the apothecia, and they rarely occur well toward the center of the thallus. The more central ones are likely to be past prime and more or less distorted.

Owing to the uncertainty of finding the sex organs and their slight or infrequent taxonomic value, we have, after working them out laboriously, decided not to burden the diagnosis with matter of so little value in determining species. Instead, we have given the results from studies of these organs toward the close of the paper where they may be accessible to those who may wish to consult them. Though the sexual tracts are not of sufficient diagnostic worth to warrant lengthening the diagnoses considerably in order to include them, it is true that critical workers on the *Collemaceae* must hereafter take these structures into account. Miss Bachman's results (1 and 2) and our own findings from several regions widely separated (Figs. 14 and 20) prove that forms so much alike with respect to somatic characters and their method of modifying the algal-host colonies may differ so much with respect to the sexual tracts that they can scarcely belong to the same genera (Pls. III and IV). This means that critical workers on the *Collemaceae* must know at least the general nature of the reproductive tracts in every specimen in which they can be found in order to be reasonably certain that forms so much alike otherwise do not differ greatly with respect to the sex organs and their behavior. Some of the minor differences in size and form of the sexual tracts within the family may be seen by consulting our figures (Pls. III and IV), and the measurements given in the descriptions of the sex organs. Our work on these areas in *Synechoblastus* illustrates the rather slight differences within the species studied from this genus. The differences in size of ordinary spermatia and the internal male reproductive cells found in certain of the *Collemaceae* may be seen by comparing Figs. 14, 20, 21, 22, and 23.

One of the writers of the present paper had Miss Bachman's material for examination during the progress of her studies. It seemed certain enough that she was working on *Collema pulposum* until the peculiarities with respect to the morphology and the behavior of the sex organs were discovered. It then became apparent that her plants could not be *Collema pulposum,* if those previously studied by Stahl (7) and Sturgis (8) are this species. Unfortunately, the reproductive areas can be studied successfully from herbarium material so seldom that it is doubtful whether microscopic study of the type of the genus *Collema* and the type specimen of *Collema pulposum* would help to decide which plants are like the types with respect to the sexual tracts. To attempt to treat in this paper the material with internal sex organs found in Ohio would be premature. One of the writers will continue with taxonomic studies of the material already examined by us from Wisconsin, Iowa, Minnesota, Ohio, Missouri, and New York, with any other that we may discover, while the other author pursues further cytologic investigations.

The thalli of members of the *Collemaceae* are composed entirely of hyphae. The hyphae are commonly long-celled and loosely interwoven in such fashion as to form a mycelial structure, which usually composes the larger portion of the somatic areas. In the hypothecia and the exciples, the hyphæ are closely interwoven. In these areas, the cells of the hyphæ may be long, or they may be approximately isodiametrical and so closely placed as to exclude interhyphal spaces. In *Leptogium* and *Mallotium* there is a distinct cortex, usually one layer of cells in thickness (Fig. 1), composed of a layer of roughly isodiametric end-cells of hyphæ which extend from the dorsal to the ventral surface. Lindau (5) has proposed the term plectenchyma for the densely interwoven parenchymatoid hyphal tissues of fungi and has distinguished two kinds, the paraplectenchyma with cells roughly isodiametrical and the prosoplectenchyma with the cells more or less elongated and the ends narrowed. The paraplectenchyma is found in the cortices in certain genera of the *Collemaceae* and in the exciples and the hypothecia of certain species. The prosoplectenchyma is rarely seen in the plants which we have studied, and we have not attempted to differentiate. Loosely interwoven hyphæ with much elongated cells we have designated mycelial structure. The mycelial structure is probably present in the medullæ of all somatic tracts within the group, though a plectenchymatoid appearance is sometimes seen in the medulla in instances in which the hyphæ are so densely interwoven and so interspersed with algal-host cells as to obscure the structure. The hypothecia and the exciples may be composed of ordinary long-celled, but closely interwoven hyphæ (Fig. 9), or they may be plectenchymatous (Fig. 10). The hyphæ of the medullæ extend in various directions (Fig. 1), and the number that lie perpendicular to the surfaces of the thallus is usually largest about the apothecia and toward the margins of the thalli. This distribution gives strength to the thalli.

Perhaps no part of our work presented greater difficulty than determining whether certain hypothecia, exciples, and medullæ, or certain portions of these structures, are plectenchymatous or whether they are composed of closely interwoven hyphæ which have elongated cells. Transitional conditions occur, and one may easily mistake interwoven hyphæ with elongated cells for a plectenchyma when the hyphæ are closely packed. We found a plectenchymatoid appearance in the medullæ of certain specimens of *Leptogium tremelloides* (Fig. 2) and *Leptogium chloromelum,* and even in the same section, certain portions may show a plainly mycelial structure while others, in which the hyphæ are densely packed, may appear like a plectenchyma. Careful maceration failed to show a true plectenchyma in any instance in our specimens of these two species. Other species are said by certain workers to be plectenchymatous throughout, but it may well be doubted whether this is true. We examined *Leptogium tenuissimum,* which is figured in Engler and Prantl as plectenchymatous throughout, but found a plainly but densely mycelial structure toward the lower surface. *Leptogium plectenchymum,* described in this paper, varies greatly with respect to position and amount of plectenchyma, but we found no specimens which were wholly plectenchymatous in the vegetative areas. Certain hypothecia and exciples present greater difficulty than any of the medullæ that we have examined, and only the use of high powers, the oil-immersion lens, and careful maceration will solve the problem in many instances. We do not wish to leave the impression that such obstacles arise in the study of all the species of the *Collemaceae.* On the other hand, the typical plectenchyma (Fig. 3) and the typical mycelial structure (Fig. 1) are readily recognizable.

The apothecia of all of the *Collemaceae* studied possess a more or less strongly developed exciple. Surrounding the exciple and often extending above it is a thalloid margin, composed of elements of the lichen thallus, with which algal-host filaments are intermingled. The thalloid margin is sometimes absent or overgrown, when the exciple is naked as in many other ascomycetes. In some of the species, one must resort to the oil-immersion lens to demonstrate the exciple. This structure extends below into the hypothecium, which is much thicker as a rule and is always easily demonstrable. It needs to be made clear that the thalloid margin is not a part of the apothecium, but belongs rather to the somatic tract of the lichen, and is intermingled with elements of the algal-host colony, which, in this family, obscure the real thalloid margin.

The *Collemaceae* form a very distinct group of ascomycetes, especially peculiar with respect to conditions of parasitism and resulting thallus disposition and structure. In the lower members of the family, the thallus is a mycelium pure and simple as found in *Synechoblastus* and *Collema.* In certain other genera as *Leptogium* and *Mallotium,* the mycelial structure gives way in part to a cortical plectenchyma. In rare instances, the plectenchyma extends throughout a large portion of the thallus, which, as noted above, is said by some students to be wholly plectenchymatous in some species. A plectenchyma sometimes occurs in the hypothecium and in the exciple, even in the lower members of the family, in which the vegetative areas are wholly mycelial. Hence, it seems safe to assume that the most primitive plectenchyma is that found in the fruit rather than that found in the somatic areas. About and below the apothecia of *Leptogia*, the plectenchyma is usually several layers of cells in thickness (Fig. 3), and it is similarly thickened below the apothecia in the material of *Mallotium* at hand for examination.

An interesting series of transitional conditions which indicates how a cortical plectenchyma may have arisen came to light in our studies of *Synechoblastus flaccidus* (Figs. 6, 7, and 8). Short cells at the upper and the lower ends of erect hyphæ often coalesce over limited areas of the thallus and form either a typical plectenchyma, or a structure strongly suggestive of a cortical plectenchyma. In some instances, the cells which coalesce are elongated and form a palisade which differs considerably from a true plectenchyma (Fig. 6). Over other areas the short end-cells are formed but do not cohere (Fig. 7). On account of these transitional conditions, this species is often placed in the genus *Leptogium* in herbaria. In *Leptogium chloromelum,* the plectenchymatous cortex is often poorly developed, and in some instances it is discontinuous and recalls the conditions just noted for *Synechoblastus flaccidus.* These two species bridge fairly well the gap between members of the *Collemaceae* which have no cortex and those which have one. Some of the material of *Mallotium* also showed a poorly developed and scarcely continuous cortical plectenchyma.

Sweeping statements to the effect that paraphyses are uniformly simple in many families of ascomycetes are due to the careless manner in which the examinations are made. We have not studied a species of the *Collemaceae* in which branched paraphyses do not occur (Fig. 11). In instances in which it is difficult to ascertain the structure, maceration and examination with an oil-immersion lens will always reveal branched paraphyses, often in large numbers. Though simple paraphyses occur in all of the species that we have studied, branched ones sometimes appear to be more numerous than the simple ones when one makes a careful examination.

The spores of the *Collemaceae* are hyaline and vary from simple ones to muriform conditions (Fig. 13). The occurrence of muriform spores in *Collema* and simple ones in genera that have a plectenchymatous cortex makes it probable that there are at least two lines of descent within the family, one expressed mainly in the spore evolution, and the other showing the spore evolution and also the development of a cortical plectenchyma. In separating *Synechoblastus,* with several-celled spores, from *Collema,* which has muriform spores, we are following the tendency among students of ascomycetes to give more prominence than formerly to spore characters, in limiting genera. A gradual evolution from simple spores to several-celled ones and from these to muriform types is well known in many groups of ascomycetes; and transitional conditions in which a species may have either simple or septate spores, or either several-celled or obscurely muriform ones are occasionally met. Therefore, one sometimes meets difficulties in using spore characters as taxonomic criteria in the *Collemaceae* and in some other ascomycetes. However, we have encountered no difficulty in the species treated in this paper.

The *Collemaceae* are related, with respect to apothecial and somatic structure, to the *Pannariaceae* and to the *Lecideaceae.* The difference in structure of the thallus, in the *Lecideaceae* on one side and the *Collemaceae* and the *Pannariaceae* on the other, is mainly explainable as a reaction to different hostal environment and to inorganic, substratic conditions. With respect to the sexual tracts, the *Collemaceae* are closely related to many lichens and other ascomycetes. These relationships are considered in the previous paper of this series.

Eleven genera of *Collemaceae* are recognized in Engler and Plantl's "Natürlichen Pflanzenfamilien." Of the genera recognized in Engler and Prantl, only *Physma, Leptogium,* and *Collema* are known in North America. However, there seems to be no sufficient reason for excluding the monotypic North American genus, *Hydrothyria,* from the *Collemaceae.* Seven of the foreign genera are monotypic, and the other one is ditypic. Of approximately 200 species of the *Collemaceae,* somewhat more than half occur in North America.

Thirteen species of the *Collemaceae* had been listed for Ohio when we began our work three years since. Of these, *Synechoblastus crystaspis, Collema crispum, Leptogium juniperinum* and *Mallotium myochroum* do not seem to occur in the state, the determinations being faulty or resting on insufficient or sterile material. Our studies have added seven species to the flora of Ohio, two of which are new. The total number of species now known for the state is sixteen. Besides this, the species with internal reproductive organs remains to be described. Sets of the material on which this paper is based may be found in the state herbarium and in the herbarium of Bruce Fink.

During most of the time that we have worked on the *Collemaceae* of Ohio, Miss Leafy J. Corrington has given her forenoons to the work under our direction, and we are under obligations to her for assistance.

Systematic Account

COLLEMACEAE

Thallus, with rare exceptions, composed wholly or mainly of a mycelium which penetrates throughout and usually surrounds the algal-host colony; hyphæ not attached to the cells of the hosts in any of our species; the mycelial structure surrounded, in the higher genera, by a cortical plectenchyma, usually a single layer of cells, except around and below the apothecia; attached to the substratum by hyphal rhizoids, which are usually seen only in sections; female sex organ an archicarp, differentiated into an ascogonium and a trichogyne; male sex organ usually a spermagonium, which contains spermatia, but sometimes an internal spermatium (antheridium, or antheridial conidium?); external conidia known in one member of the family; apothecia with an exciple, either plectenchymatous or of interwoven hyphæ, a hypothecium, the structure of which is usually like that of the exciple into which it is produced, and a hymenium composed of the asci and the paraphyses, the former blue and the latter yellow-brown in iodine; spores simple, several-celled, or muriform, brown in iodine; apothecia usually surrounded by a thalloid margin.

The algal host is a form of *Nostoc* and is strongly modified and transformed into a more or less plainly foliose structure, which has peculiar features of form, size, or color dependent on the transforming effect of the particular lichen parasite. The algal-host colony becomes gelatinous when wet, and the gelatinization is more marked when the alga functions as the host of a species of the *Collemaceae* which is devoid of a cortical plectenchyma.

KEY TO THE GENERA

Without a typical plectenchymatous cortex.
    Spores 2- to several-celled.................................**Synechoblastus**
    Spores muriform...**Collema**

With a typical plectenchymatous cortex.
    Rhizoids not plainly noticeable with the hand lens..........**Leptogium**
    Rhizoids plainly noticeable with the hand lens..............**Mallotium**

SYNECHOBLASTUS Trev. Caratt. Gen. Collem. 2. 1853.

Transforming the algal-host colony into a blue-green, olivaceous, or nearly black, irregular or foliose body, with the lobes often ascending or erect and covering the horizontal portions, often to the center of the colony; thallus not differentiated into a typical plectenchymatous cortex and a mycelia medulla, but the whole structure commonly mycelial and the hyphæ usually more densely disposed toward the surfaces, especially the upper surface; hyphæ hyaline, perpendicular, horizontal, and extending in various directions, straight or curved, monopodially branched; rhizoids inconspicuous, but commonly seen in sections of some of the species; apothecia scattered; disk flat to convex, red-brown to black-brown, surrounded by a thalloid margin which is sometimes overgrown; exciple either densely mycelial or plectenchymatous, usually tinged with brown; hypothecium similar in structure and color; hymenium hyaline below to pale- or darker-brown above; paraphyses hyaline at the base and gradually becoming tinged with brown toward the enlarged apex, simple or once to several times monopodially branched toward the apex or farther back, all species examined showing both simple and branched ones, the number of cells ranging from 5 to 20, the length from 45 to 115 mic., and the width from 1.5 to 5 mic.; asci clavate, the walls 0.5 to 2 mic. thick laterally and 2 to 9 mic. thick at the apex; spores hyaline, 2- to several-celled, but not muriform, 8 in each ascus and irregularly arranged in all of ours.

On account of the flexible nature of the thallus, which is devoid of a strengthening plectenchymatous cortex, the algal host becomes enlarged and more or less plainly gelatinous when moist.

KEY TO THE SPECIES OF SYNECHOBLASTUS

Spores 2-celled.
  Apothecia marginal on the densely aggregated, erect lobules....................2. **Synechoblastus pycnocarpus**
  Apothecia scattered over the surface.......1. **Synechoblastus ohioensis**

Spores more than 2-celled.
  A rudimentary plectenchymatous cortex often seen, usually sterile..............5. **Synechoblastus flaccidus**
  Wholly devoid of cortex, usually fertile.
    Spores less than 40 mic. long..........4. **Synechoblastus ryssoleus**
    Spores more than 40 mic. long........3. **Synechoblastus nigrescens**

1. **Synechoblastus ohioensis** Fink sp. nov.

Transforming the algal-host colony into a rather small, suborbicular or irregular, foliose body, which is 2 to 5 cm. across, 225 to 500 mic. thick, and rather loosely adnate, with ascending lobes, the margins of which are sometimes closely rugose lobulate, with the upper surface dark-olivaceous, varying toward black or green, with the lower surface lighter colored, and with the algal chains more numerous toward the surfaces, especially the upper; thallus of rather densely disposed hyphæ, which are somewhat uniformly distributed with their course, mainly perpendicular to the surfaces, but in part irregular, or roughly horizontal toward the center, 3 to 8 mic. wide; rhizoids well developed and commonly seen in sections of thalli; apothecia common, small to middle-sized, sessile, scattered, 0.5 to 2.5 mm. in diameter; disk flat or convex, red- to dark-brown, surrounded by an entire thalloid margin, which may extend above it or may rarely become overgrown; exciple hyaline, of interwoven hyphæ, but plectenchymatoid above; hypothecium of interwoven hyphæ, 80 to 120 mic. thick; hymenium 65 to 105 mic. thick; paraphyses frequently and variously branched; asci 55 to 65 mic. long, and 13 to 16 mic. wide; spores ovoid to ellipsoid-pointed, 2-celled, 12 to 24 mic. long and 5 to 8 mic. wide. See Fig. 25.

Found on limestone rocks near Peebles, Adams County, usually growing with mosses. The plant was collected for *Collema pulposum*, but differs considerably in its effect on the appearance of the algal-host colony and much more in its anatomical characters. This new species resembles *Synechoblastus pycnocarpus* strongly, but it modifies the algal-host colony in a different manner and has several distinct features of thallus and fruit. The plant seems to resemble *Synechoblastus texanus* (Tuck.), both in its physiological action on the algal-host colony and in its anatomical characters. Three collections were made near Peebles.

2. **Synechoblastus pycnocarpus** (Nyl.) Fink Cont. U. S. Nat. Herb. *14*[1]: 134. 1910.

Collema pycnocarpum Nyl. Syn. Lich. *1:* 115. 1858.

Transforming the algal-host colony into a rather small, suborbicular, foliose body, which is 1.5 to 6 cm. across and 150 to 875 mic. thick, the horizontal portions closely adnate and sometimes sparingly perforate, with the lobes long and more or less branched, rising toward the margin into a suberect position, the erect or ascending portions densely rugose lobulate and obscuring more or less the parts below, especially when covered with apothecia, with the upper surface olivaceous varying toward green or black, and sometimes granulate, with the lower surface lighter colored, and with the algal chains distinctly more numerous toward the surfaces; thallus of hyphæ which are densely disposed toward the surfaces but somewhat scattered toward the center, variously placed and in part perpendicular or horizontal, the latter especially toward the center, 2 to 4 mic. wide; rhizoids seen in large numbers in certain sections of the thallus; apothecia small, numerous, sessile, marginal on erect or ascending lobules, 0.4 to 0.8 mm. in diameter; disk flat to convex, brown or red-brown, surrounded by an entire thalloid margin, which does not extend above the disk and is sometimes overgrown; exciple of interwoven hyphæ, tinged with brown; hypothecium of interwoven hyphæ, 33 to 85 mic. thick; hymenium 55 to 85 mic. thick; paraphyses frequently and variously branched; asci 45 to 62 mic. long and 10 to 14 mic. wide; spores ovoid to ellipsoid-pointed, 2-celled, 11 to 20 mic. long and 3.5 to 6.5 mic. wide. See Figs. 9, 11, 18, and 24.

Widely distributed in the state, but not common. On tree trunks. Examined from areas about Peebles, Springfield, Amanda, Cedar Swamp, Paint, Prospect, and Columbus.

3. **Synechoblastus nigrescens** (Huds.) Stizenb. Ber. St. Gall. Ges. Naturw. *1861-1862*: 144. 1862.

Lichen nigrescens Huds. Fl. Angl. 450. 1762.

Transforming the algal-host colony into a middle-sized, orbicular or irregular foliose body, which is 2 to 7 cm. across, 60 to 185 mic. thick, and closely adnate, with the upper surface closely beset with pustules, on many of which apothecia are situated, or with the pustules largely replaced by radiating ridges, with short, rounded, entire, and usually somewhat raised lobes, with the upper surface olive-green and blackening, with the lower surface lighter colored and marked by depressions which correspond with the pustules or the ridges of the upper surface, and with the algal chains somewhat more numerous toward the upper surface; thallus of hyphæ which are densely disposed, somewhat uniformly distributed with course largely perpendicular or horizontal, and 1 to 2.5 mic. wide; rhizoids rarely seen in the sections; apothecia rather small, numerous, sessile, crowded toward the center of the thallus, which is sometimes obscured by them, 0.4 to 1.2 mm. in diameter; disk flat or convex, brown or red-brown and surrounded by a thin thalloid margin, which is sometimes overgrown; exciple plectenchymatous, tinged with brown; hypothecium plectenchymatous below, of interwoven hyphæ above, 40 to 65 mic. thick; hymenium 85 to 115 mic. thick; paraphyses sometimes anastomizing by a bridge; asci 65 to 85 mic. long and 14 to 22 mic. wide; spores 4- to several-celled, long-fusiform to acicular, 40 to 70 mic. long and 3.5 to 6.5 mic. wide. See Figs. 12 and 13.

Known in Ohio only through specimens collected by T. G. Lea near Cincinnati, in 1841. However, the plant should occur in other portions of the state. On the trunks of trees.

4. **Synechoblastus ryssoleus** (Tuck.) Fink Cont. U. S. Nat. Herb. *14*^{1}: 135. 1910.

Collema nigrescens ryssoleum Tuck. Lich. Calif. 34. 1866.

Transforming the algal-host colony into a rather small, suborbicular, foliose, membranaceous body, which is 2 to 5 cm. across, 60 to 200 mic. thick, and rather smooth, with rounded, ascending lobes, with plicate, undulate and crisped margins, with the upper surface olivaceous to black-brown and rugose-papulose, with the lower surface lighter colored and reticulate, and with the algal chains somewhat more numerous toward the surfaces; thallus of densely disposed hyphæ, which are more numerous toward the surfaces and largely perpendicular, but in part horizontally or irregularly placed, 2 to 5 mic. wide; rhizoids seldom seen in the sections; apothecia minute to middle-sized, numerous but scattered, sessile, 0.2 to 1.5 mm. in diameter; disk brown or red-brown, flat or convex, surrounded by a thin, entire thalloid margin, which is sometimes overgrown; exciple of interwoven hyphae tinged with brown; hypothecium of interwoven hyphæ, 40 to 85 mic. thick; hymenium 85 to 95 mic. thick; asci 60 to 85 mic. long and 12 to 20 mic. wide; spores long ellipsoid-pointed, 6-celled, 22 to 34 mic. long and 4 to 6 mic. wide.

A single specimen was collected by W. A. Kellerman, in Delaware County. The specimen is sterile and without number. On tree trunks. The microscopic apothecial characters were taken mainly from *Lichenes Boreali-Americani,* No. 199.

5. **Synechoblastus flaccidus** (Ach.) Trev. Caratt. Gen. Collem. 1853.

Lichen flaccidus Ach. Vet. Akad. Handl. *16*: 14. 1795.

Transforming the algal-host colony into a middle-sized, suborbicular or irregular foliose body, which is 3 to 7 cm. across, 40 to 185 mic. thick, and rather loosely attached to the substratum, with rather wide, rounded, entire, and often imbricated lobes, with the upper surface olivaceous, varying toward black or green, usually granulate, with the lower surface commonly lighter colored, and with the algal cells somewhat more numerous toward the upper surface; thallus of densely disposed hyphæ, which extend in various directions and are 2.5 to 4 mic. wide, those perpendicular to the surface of the thallus often passing at one end or at both ends into short, enlarged cells, or into branches, the end cells of which are short and wide and sometimes cohere laterally to form a true plectenchyma over limited areas; rhizoids rarely seen in the sections; apothecia rare, small to middle-sized, sessile, 0.5 to 1.5 mm. in diameter; disk concave to slightly convex, brown or red-brown, surrounded by an entire, often granulate thalloid margin, which may extend above it; exciple plectenchymatous, tinged with brown; hypothecium plectenchymatous below, of interwoven hyphæ above, 34 to 88 mic. thick; hymenium 85 to 125 mic. thick; asci rather large, 80 to 110 mic. long and 14 to 21 mic. wide; spores long ellipsoid-pointed, 4- to 6-celled, 28 to 40 mic. long and 5 to 9 mic. wide. See Figs. 6, 7, 8, 13, and 17.

Widely distributed in the state. On trees and rarely on rocks. Examined from areas about Amanda, Eaton, Oxford, Peebles, Paint, and Orwell.

COLLEMA (Hill.) Web. in Wig. Prim. Fl. Hols. 89. 1780.

Transforming the algal-host colony into a squamulose or an irregularly foliose body, with the upper surface olivaceous, varying toward green or black and the lower surface somewhat lighter colored; thallus wholly mycelial and the hyphæ more densely disposed toward the surfaces; hyphæ hyaline, variously and often densely disposed, straight or curved, monopodially branched; rhizoids inconspicuous but commonly seen in sections; apothecia commonly scattered; disk varying from concave to convex, from light brown to dark brown, surrounded by a thalloid margin, which is rarely overgrown; exciple either densely mycelial or plectenchymatous, usually hyaline; hypothecium usually of interwoven hyphæ, hyaline below to pale brown above; hymenium hyaline below to brown above; paraphyses hyaline at the base and tinged with brown toward the somewhat enlarged apex, simple or sometimes monopodially branched toward the apex or farther back, all species showing both simple and branched ones, the number of cells varying from 5 to 9, the length from 55 to 160 mic., the diameter from 1.5 to 4 mic.; asci clavate, the walls 9.5 to 2.5 mic. thick laterally and 5 to 13 mic. thick at the apex; spores hyaline, ellipsoid, muriform, 8 in each ascus, irregularly arranged.

KEY TO THE SPECIES OF COLLEMA

Attached to calcareous rocks.
Spores usually less than 8 mic. wide..............4. **Collema plicatile**
Spores usually more than 8 mic. wide............5. **Collema furvum**

Not attached to calcareous rocks.
On calcareous soil and on mosses, usually over calcareous rocks.
Thallus and transformed algal-host colony 200 to 750 mic. thick..............................1. **Collema pulposum**
Thallus and algal-host colony less than 100 mic. thick ....2. **Collema tenax**
On tree trunks....................................3. **Collema microphyllum**

1. **Collema pulposum** (Bernh.) Ach. Lich. Univ. 632, pl. 14. f. 9. 1810.

Lichen pulposus Bernh. Journ. Bot. Schrad. *1799*^{1}*:* pl. 1. f. 1. 1799.

Transforming the algal-host colony into a middle-sized, orbicular or more or less irregular body, which is 1.5 to 8 cm. across, 200 to 750 mic. thick, and closely attached to the substratum, with thick, entire or repand-crenate and often imbricated, rosulate lobes, which are often reduced in the central portions, to mere granules, with the upper surface olivaceous, varying toward black, with the lower surface scarcely lighter colored, and with the algal chains more numerous toward the surfaces; thallus of scattered or rather densely disposed hyphæ with course largely irregular, but roughly horizontal toward the center, 1 to 4 mic. wide; rhizoids numerous at the scattered points of attachment; apothecia common, small to middle-sized, adnate or sessile, 0.6 to 2.5 mm. in diameter; disk concave to slightly convex, red-brown, surrounded by an entire or rarely crenate thalloid margin, which extends above it, or is rarely overgrown; exciple thin, of interwoven hyphæ, tinged with brown; hypothecium of interwoven hyphæ, tinged with brown, 40 to 80 mic. thick; hymenium 90 to 125 mic. thick; asci 70 to 90 mic. long and 11 to 21 mic. wide; spores longitudinally 4- to 5-celled and transversely 2-celled, 17 to 32 mic. long and 6 to 11 mic. wide. See Figs. 9, 13, 15, 16, and 21.

Widely distributed in southern Ohio. On calcareous earth, or on mosses over calcareous rocks. Examined from areas about Oxford, Cincinnati, Eaton, Fultonham, and Peebles. Not previously reported for Ohio, but collected by T. G. Lea near Cincinnati, in 1841.

2. **Collema tenax** (Sw.) Ach. Lich. Suec. 128, 237. 1798.

Lichen tenax Sw. Nov. Act. Soc. Sci. Ups. *4:* 249. 1784.

Transforming the algal-host colony into a small to middle-sized, orbicular or more or less irregular body, which is 0.5 to 7 cm. across, 65 to 85 mic. thick, and closely attached to the substratum, usually crenately lobed and imbricated, but sometimes depauperate and reduced to squamules when attached directly to rocks, with the upper surface olivaceous, varying toward black, with the lower surface scarcely lighter colored, and with the algal chains numerous and somewhat evenly distributed; thallus of densely disposed hyphæ, which are often perpendicular to the surfaces and are 2.5 to 4. mic. wide; rhizoids numerous at the points of attachment; apothecia common, small to middle-sized, sessile or adnate-immersed, 0.5 to 2 mm. in diameter; disk concave to slightly convex, red-brown and darker, surrounded by an entire or a crenate thalloid margin, which does not extend above it; exciple hyaline, of interwoven hyphæ; hypothecium of interwoven hyphæ, 80 to 95 mic. thick; hymenium 130 to 160 mic. thick; asci 65 to 75 mic. long and 16 to 20 mic. wide; spores longitudinally 4- to 5-celled, transversely 2-celled, 16 to 21 mic. long and 7 to 10 mic. wide.

Collected near Paint, by Bruce Fink, No. 460. Usually on calcareous soil over rocks, often growing with mosses. Ours a depauperate condition on calcareous rocks. Previously recorded for Ohio, but we have not seen the specimens.

3. **Collema microphyllum** Ach. Lich. Univ. 630. 1910.

Transforming the algal-host colony into a minute, suborbicular or irregular body, which is 0.1 to 1 cm. across, 110 to 160 mic. thick, and closely adnate or sometimes raised at the margin, with the marginal lobes rounded and those toward the center reduced, granulate-crenate, and often imbricate, with the upper surface black-olive, and with the algal chains somewhat more numerous toward the upper surface; thallus of densely disposed, much branched hyphæ, which are uniformly distributed, extend in various directions, and are 2.6 to 4 mic. wide; rhizoids hyaline, numerous at certain points, especially under the apothecia; apothecia numerous, minute or small, sessile, or adnate, 0.3 to 0.6 mm. in diameter; disk concave to flat, red- to dark-brown, surrounded by an entire thalloid margin which does not extend above it and often becomes overgrown; exciple plectenchymatous, hyaline; hypothecium plectenchymatous below and of interwoven hyphæ above, 55 to 80 mic. thick; hymenium 90 to 120 mic. thick; asci 85 to 95 mic. long and 21 to 26 mic. wide; spores longitudinally 4-celled and transversely 2-celled, 18 to 25 mic. long and 9 to 13 mic. wide. See Figs. 10, 12, and 23.

Collected near Peebles, by Bruce Fink, No. 64. On tree trunks. Not previously recorded for Ohio.

4. **Collema plicatile** Ach. Lich. Suec. 129, 237. 1798.

Lichen plicatilis Ach. Vet. Akad. Handl. *16*: 11. pl. 1. f. 2. 1795.

Transforming the algal-host colony into a small, irregular or suborbicular, somewhat coriaceous body, which is 0.4 to 2.5 cm. across, 185 to 370 mic. thick, and loosely attached to the substratum, with more or less imbricated, ascending or erect lobes with plicate-crisped margins, with the upper surface black-olive, with the lower surface scarcely lighter colored, and with the algal chains scattered toward the center but numerous toward the surfaces; thallus of densely and variously disposed hyphæ, which are 3 to 5 mic. wide; rhizoids rare, except at the points of attachment of the thallus to the substratum; apothecia small, sessile, scattered, 0.5 to 1 mm. in diameter; disk concave to flat, red- to dark-brown, surrounded by an entire thalloid margin, which does not extend above it; exciple very thin, of interwoven hyphæ, tinged with brown; hypothecium of interwoven hyphæ, light brown, 90 to 105 mic. thick; hymenium 130 to 160 mic. thick; asci 80 to 95 mic. long and 14 to 18 mic. wide; spores longitudinally 4-celled, becoming transversely 2-celled, 24 to 30 mic. long and 5 to 9 mic. wide.

Collected near Peebles, by Bruce Fink, No. 94. On calcareous rocks. Not previously recorded for Ohio.

5. **Collema furvum** Ach. Lich. Suec. 132, 236. 1798.

Lichen furvus Ach. Lich. Suec. 132. 1798.

Transforming the algal-host colony into a suborbicular or irregular, small or middle-sized body, which is 0.7 to 5 cm. across, 145 to 310 mic. thick, and loosely attached to the substratum, with rounded or somewhat irregular, entire and ascending lobes, which have undulate or crenulate and somewhat crisped edges, with the upper surface black-olive and covered with granules, with the lower surface lighter colored, and with the algal chains somewhat more numerous toward the surfaces; thallus of densely and irregularly disposed hyphæ, which are infrequently either perpendicular or horizontal to the surface, 1.3 to 5 mic. wide; rhizoids numerous at the points of attachment of the thallus to the substratum; apothecia small, few and scattered, sessile, 0.3 to 1 mm. in diameter; disk concave or flat, light brown, becoming dark, surrounded by an entire thalloid margin, which may extend slightly above it; exciple plectenchymatous, hyaline; hypothecium plectenchymatous below, of interwoven hyphæ above, 90 to 160 mic. thick; hymenium 105 to 120 mic. thick; asci 90 to 105 mic. long and 20 to 32 mic. wide; spores longitudinally 4- to 6-celled, transversely 2- to 3-celled, 17 to 26 mic. long and 8 to 12 mic. wide. See Fig. 13.

Collected near Peebles, by Bruce Fink, No. 184. On calcareous rocks. Not previously recorded for Ohio.

LEPTOGIUM Ach.; S. F. Gray, Nat. Arr. Brit. Pl. *1:* 400. 1821

Transforming the algal-host colony into a foliose, usually lead-colored or olivaceous body, which is variously lobed and sometimes granulate or isidioid branched, and in which the algal-host chains are commonly more numerous toward the upper surface of the colony; thallus of a plectenchymatous cortex surrounding a medulla which is mainly or wholly mycelial, or rarely more largely plectenchymatoid; hyphæ of the medulla hyaline, straight or curved, for most part densely and variously disposed, more or less branched monopodially; plectenchymatous cortex usually well developed and of a single layer of cells, except around and below the apothecia, where it is usually several layers of cells in thickness; rhizoids rarely seen; apothecia usually scattered; the disk commonly brown and surrounded by an entire thalloid margin; exciple almost always in part or wholly plectenchymatous and usually hyaline; hypothecium hyaline below to pale brown above, more often plectenchymatous; hymenium hyaline below to pale- or darker-brown above; paraphyses hyaline toward the base and tinged with brown toward the slightly enlarged apex, all species examined showing some simple ones and others one- to several-times monopodially branched near the apex or farther back, ranging from 60 to 160 mic. long, from 2 to 3.5 mic. wide, and from 6- to 14-celled in the species examined; asci usually clavate, 65 to 105 mic. long and 12 to 21 mic. wide, the walls 0.5 to 2 mic. thick laterally, and 2 to 11 mic. thick at the apex (thicker in *Leptogium lacerum*); spores hyaline, becoming muriform, 8 in an ascus in all of ours, irregularly arranged.

On account of the rigid nature of the thallus, due to the presence of a plectenchymatous cortex, the algal-host colony does not become so much enlarged and so plainly gelatinized when moist as does the same host when parasitized by *Synechoblastus* or *Collema*, genera which are less rigid because of absence of a cortex.

KEY TO THE SPECIES OF LEPTOGIUM

Plectenchymatous cortex of several layers of cells around the apothecia.

Spores 4 cells in length.
Exciple plectenchymatous.................5. **Leptogium plechtenchymum**

Exciple of interwoven hyphæ, but often more or less plectenchymatoid..........4. **Leptogium chloromelum**

Spores usually more than 4 cells in length.
Medulla plainly mycelial...................1. **Leptogium pulchellum**

Medulla of densely interwoven hyphæ, and the structure often plectenchymatoid....3. **Leptogium tremelloides**

Plectenchymatous cortex of one or rarely two layers of cells around the apothecia......2. **Leptogium lacerum**

1. **Leptogium pulchellum** (Ach.) Nyl. Syn. Lich. *1*: 123. 1858.
Collema pulchellum Ach. Syn. Lich. 321. 1814.

Transforming the algal-host colony into a rather large, suborbicular body, which is 4 to 12 cm. across, 90 to 265 mic. thick and closely adnate, with the marginal lobes free and somewhat raised, with the upper surface lead-colored and thrown into delicate, plicate wrinkles, with the lower surface lighter colored, similarly wrinkled, and more or less pitted, with the lobes rounded and sometimes imbricated, with entire or undulate margins, and with the algal chains more numerous toward the surfaces, especially the upper; medulla of scattered hyphæ, which are in part irregularly arranged and in part perpendicular to the surfaces, the latter arrangement more noticeable toward the margins, 1.75 to 2.6 mic, wide, and slightly more numerous toward the upper surface; cells of the upper cortex 4 to 8 mic. long and 4 to 7.5 mic. wide, those of the lower cortex distinctly smaller, the cortex several cells thick around the apothecia; rhizoids rarely seen in the sections; apothecia common, small to middle-sized, 0.5 to 2 mm. in diameter, sessile or raised on a pseudostipe, and surrounded by a thalloid margin; disk flat and light- or darker-brown; exciple plectenchymatous; hypothecium plectenchymatous below, of interwoven hyphæ above, 90 to 140 mic. thick; hymenium 80 to 105 mic. thick; spores ellipsoid to ellipsoid-pointed, longitudinally 6-celled, transversely 2- to 4-celled, 18 to 33 mic. long and 9 to 16 mic. wide. See Figs. 1, 3, 5, and 13.

Generally distributed over the state, but not common. On the trunks of trees, and rarely on rocks. Examined from areas about Peebles, Washington C. H., Springfield, Paint, Cedar Swamp, Georgeville, Sugar Grove, Chester Hill, and Columbus.

2. **Leptogium lacerum** (Retz.) S. F. Gray, Nat. Arr. Brit. Pl. *1*: 401. 1821.

Lichen lacer Retz. Fl. Scand. Prodr. 228. 1774.

Transforming the algal-host colony into a middle-sized, suborbicular or irregular body, which is 1.5 to 7 cm. across, 60 to 210 mic. thick, and reticulately wrinkled, with the closely adnate horizontal portions obscured by ascending and expanding lobes, with the margins sinuate or more often finely jagged and lacerately fringed, with the upper surface lead-colored to olive-brown, with the lower surface scarcely lighter colored, and with the algal chains more numerous toward the upper surface; medulla of densely disposed and uniformly distributed hyphæ, which are 2.6 to 5 mic. wide and extend in various directions; cells of the upper cortex 8 to 13 mic. long and 11 to 13 mic. wide, those of the lower cortex scarcely differing in size; cortex rarely thickened to two layers of cells around and below the apothecia; rhizoids rarely seen in the sections; apothecia rare, small to middle-sized, sessile, 0.4 to 1.5 mm. in diameter; disk flat or concave, red-brown, surrounded by a thalloid margin, which does not extend above it and sometimes becomes concolorous, giving a biatoroid appearance; exciple and hypothecium plectenchymatous, the latter 125 to 170 mic. thick; hymenium 140 to 175 mic. thick; asci clavate or rarely obclavate, 115 to 130 mic. long, and 25 to 35 mic. wide, with the walls 2 to 3 mic. thick laterally and 20 to 25 mic. thick at the apex; spores ellipsoid and sometimes pointed, longitudinally 8- to 12-celled, transversely 2- to 4-celled, 27 to 46 mic. long and 11 to 18 mic. wide. See Fig. 13.

Widely distributed in the state, but rarely fruited. On rocks among mosses. Examined from areas about Eaton, Paint, Peebles, Oxford, Collinsville, Fultonham, Kelley's Mills, Prospect, and Springfield.

3. **Leptogium tremelloides** (L.) S. F. Gray, Nat. Arr. Brit. Pl. *2*: 400. 1821.

Lichen tremelloides L. Suppl. Pl. 450. 1781.

Transforming the algal-host colony into a middle-sized, suborbicular body, which is 3 to 8 cm. across, 65 to 210 mic. thick, and rather closely adnate, with ascending and often imbricated lobes, with entire or finely undulate or dentate, crisped and irregular margins, with the upper surface lead-colored and beset more or less with isidioid branchlets, which may pass into minute lobules, with the lower surface somewhat lighter colored, and with the algal chains more numerous toward the upper surface; medulla of densely interwoven and uniformly distributed, vertically and variously disposed hyphæ, which are 2.4 to 2.7 mic. wide, often in part or wholly plectenchymatoid; cells of the upper cortex 5 to 10 mic. long and 5 to 8 mic. wide, those of the lower cortex scarcely differing in size; cortex several cells in thickness around and below the apothecia; rhizoids rarely seen in the sections; apothecia small to middle-sized, scattered, sessile or on a short pseudostipe, 0.5 to 1.7 mm. in diameter; disk from slightly concave to slightly convex, brown, surrounded by an entire or an irregular thalloid margin, which is sometimes overgrown; exciple at least very largely of interwoven hyphæ; hypothecium of interwoven hyphæ, except perhaps at the lower limit, where it is plectenchymatous or plectenchymatoid, 80 to 100 mic. thick; hymenium 90 to 115 mic. thick; spores ovoid-ellipsoid to ellipsoid-pointed, longitudinally 4- to 6-celled, transversely 2- to 3-celled, 18 to 32 mic long and 7 to 12 mic. wide. See Fig. 12.

A rare plant in Ohio, the distribution of which is not well known.

On rocks and on trunks of trees. Examined from areas about Columbus, Sugar Grove, Peebles, and Eaton.

4. **Leptogium chloromelum** (Sw.) Nyl. Syn. Lich. *1*: 128. 1858.

Lichen chloromelos Sw. Fl. Ind. Occ. *3:* 1892. 1808.

Transforming the algal-host colony into a middle-sized, suborbicular or irregular, thin body, which is 2 to 7 cm. across and 50 to 185 mic. thick, with sometimes scattered, usually isidioid-granulate, frequently imbricate, ascending lobes, with crisped, undulate, or isidioid-lobulate margins, with the upper surface lead-colored varying toward green or olivaceous, with the lower surface scarcely lighter colored, and with the algal chains somewhat evenly distributed; medulla of densely, uniformly, and variously disposed hyphæ, which are 2 to 5 mic. wide, sometimes plectenchymatoid in part or throughout; cortex rather poorly developed and not always continuous, the cells of the upper cortex 7 to 16 mic. long and 4.5 to 12 mic. wide, those of the lower cortex scarcely differing in size; cortex several cells in thickness around and usually below the apothecia; rhizoids often seen in sections, especially under the apothecia; apothecia commonly present and often numerous, small to middle-sized, sessile, 0.5 to 1.5 mm. in diameter; disk slightly concave to slightly convex, brown, surrounded by a granulate, entire or irregular thalloid margin, which may extend above it; exciple and hypothecium of interwoven hyphæ, but both structures wholly or in part plectenchymatoid, the latter 80 to 105 mic. thick; hymenium 105 to 155 mic. thick; spores ovoid to ellipsoid-pointed, longitudinally 4-celled, transversely 2-celled, 15 to 30 mic. long and 8 to 13 mic. wide. See Figs. 4, 19, and 22.

Widely distributed in the state, but infrequent. On rocks and tree trunks. Examined from areas about Springfield, Scipio, Oxford, Paint, Mineral Springs, and Peebles.

5. **Leptogium plectenchymum** sp. nov.

Transforming the algal-host colony into a small or middle-sized, suborbicular or irregular body, which is 0.8 to 7 cm. across, 35 to 110 mic. thick, and somewhat loosely adnate, with ascending and often imbricated lobes, with entire or irregular, often minutely lobulate margins, with the upper surface lead-colored, with the lower surface somewhat lighter colored, and with the algal chains somewhat evenly distributed; medulla of densely and uniformly distributed, vertically and variously disposed hyphæ, which are 3 to 5 mic. wide; cells of the upper cortex 9 to 19 mic. long and 5 to 14 mic. wide, those of the lower cortex somewhat smaller; cortex thickened from 2 to several layers of cells around and below the apothecia, the whole area below the apothecia sometimes being plectenchymatous; the occurrence of the plectenchymatous cortex varying greatly, this structure being in some specimens thickened only under the apothecia, while in others it is thickened from 2 to 8 or 9 layers of cells around the apothecia, the thickening sometimes passing outward 500 mic. or more in all directions from each apothecium; rhizoids numerous under the apothecia; apothecia middle-sized or large, sessile, scattered, 0.5 to 3 mm. in diameter; disk flat or convex, red-brown, surrounded by an entire or irregular thalloid margin, which often becomes concolorous with the disk and resembles in appearance a true exciple; exciple plectenchymatous, slightly tinged with brown, often passing imperceptibly into the thickened plectenchymatous cortex about the apothecium; hypothecium usually composed wholly of interwoven hyphæ, but sometimes in part plectenchymatous below, 45 to 115 mic. thick; hymenium 150 to 170 mic. thick; paraphyses narrow, 1 to 1.5 mic. wide; spores ovoid-ellipsoid to ellipsoid-pointed, longitudinally 4-celled, becoming transversely 2-celled, 22 to 30 mic. long and 8 to 14 mic. wide. See Fig. 13.

Collected three times near Oxford, by Bruce Fink. On damp clay.

MALLOTIUM Ach.; S. F. Gray, Nat. Arr. Brit. Pl. *1:* 399. 1821.

Transforming the algal-host colony into a middle-sized or large, foliose, lead-colored to black-green body, which has large, often more or less granulate, sometimes rugose lobes, in which the algal chains are commonly more numerous toward the upper surface of the colony; thallus of a mycelial medulla and a plectenchymatous cortex; medulla of hyaline, usually densely and variously disposed hyphæ, which are somewhat uniformly distributed, straight or curved, more or less branched monopodially; cortex of one layer of cells, except around and below the apothecia where there may be two or more layers of cells, not so well developed as in *Leptogium,* and sometimes difficult to demonstrate over certain areas of the thallus; rhizoids numerous and strong, appearing as a dense, light-colored nap, which usually covers the whole lower surface and forms the chief differential character of the genus; apothecia scattered; the disk usually brown and commonly surrounded by a thalloid margin; exciple and hypothecium wholly or largely of interwoven hyphæ, but both or the latter may be at least partly plectenchymatous; hymenium pale below and light-brown above; paraphyses hyaline toward the base and tinged with brown toward the more or less enlarged apex; asci usually clavate; spores hyaline, becoming muriform.

Thallus somewhat thicker than in *Leptogium* and rigid enough to overcome largely the tendency of the algal-host colony to gelatinize conspicuously when moist.

1. **Mallotium saturninum** (Dicks.) Mass. Mem. Lich. 95. pl. 18. f. 114. 1853.

Lichen saturninus Dicks. Pl. Crypt. Brit. *2:* 21. pl. 6. f. 8. 1790.

Transforming the algal-host colony into a rather large, suborbicular or irregular body, which is 4 to 15 cm. in diameter, 80 to 250 mic. thick, and somewhat ascending, rounded, subentire, or undulate, with the upper surface lead-colored varying toward olivaceous or black, more or less granulate and sometimes rugose, and the lower surface clothed with light-colored rhizoids, which form a delicate nap, and with the algal chains more numerous toward the upper surface of the colony; medulla of somewhat densely and uniformly disposed hyphæ, which are 2.5 to 5 mic. in diameter, in part irregularly arranged, but many of them roughly perpendicular while others toward the center of the thallus tend toward a horizontal position; cortex not always well developed and distinct, cells of the upper cortex 5 to 8 mic. long and 4.5 to 5 mic. wide, those of the lower cortex slightly smaller; apothecia rare, middle-sized, subsessile, 1 to 2 mm. in diameter, the disk flat and red-brown, surrounded by a more or less granulate and irregular thalloid margin; spores ellipsoid, becoming muriform, 23 to 30 mic. long and 7 to 9 mic. wide.

Known to us from Ohio only through No. 572, E. E. Bogue, collected near Columbus. Some of the specimens distributed under this number are in part or wholly *Synechoblastus flaccidus*. The only specimen seen was sterile, and the apothecial characters are taken from Tuckerman. We have never seen any American specimens in fruit. On tree trunks, and rarely on rocks.

Descriptions of Sex Organs.

Ascogonia coiled, hyaline, single or in groups; trichogynes usually passing directly or indirectly to and above the surface, one from each ascogonium; spermagonia marginal or submarginal; basidia of short cells, more or less branched; spermatia hyaline, one-celled, oblong-constricted, located on the ends and sides of the basidia. Internal male sex organs present in an Ohio species not yet named.

Synechoblastus pycnocarpus. Ascogonia on young lobes, 40 to 215 mic. below the surface, horizontal diameter 20 to 42 mic., vertical diameter 40 to 215 mic., 10- to 18-or more-celled, cells 5 to 17 mic. long and 3 to 8 mic. wide; trichogynes extending 15 to 30 mic. above the surface, where branched or unbranched, 85 to 265 mic. long, cells 7 to 59 mic. long and 3 to 7 mic. wide, the two distal cells much longer than the others; spermagonia occurring with the archicarps, horizontal diameter 55 to 200 mic., vertical diameter 55 to 205 mic.; basidia becoming 20-or more-celled, cells 3.5 to 8 mic. long and 3 to 6 mic. wide; spermatia 2 to 4 mic. long and 0.5 to 1 mic. wide, some seen as low as the fifth cell from the tip of the basidium. See Figs. 18 and 24.

Synechoblastus ryssolcus. Ascogonia 46 to 95 mic. below the surface, horizontal diameter 19 to 28 mic., vertical diameter 17 to 31 mic., 7- to 15-celled, cells 5 to 9 mic. long and 4 to 7 mic. wide; trichogynes not seen; horizontal diameter of spermagonia 55 to 155 mic., vertical diameter 65 to 125 mic.; basidia 7- to 12-or more-celled, cells 4 to 6 mic. long and 2 to 5 mic. wide; spermatia 2 to 3 mic. long and 1 mic. wide.

Synechoblastus flaccidus. Ascogonia 50 to 60 mic. below the surface, horizontal diameter 14 to 22 mic., vertical diameter 12 to 20 mic., many-celled, cells 6 to 7 mic. long and 4 to 5 mic. wide; trichogynes extending about 8 mic. above the surface, unbranched, 56 to 65 mic. long, cells 10 to 11 mic. long and 4 to 5 mic. wide; spermagonia submarginal on young lobes, horizontal diameter 150 to 165 mic., vertical diameter 105 to 150 mic., basidia 6- to 15-celled, cells 2 to 5 mic. long and 3 to 5 mic. wide; spermatia 2 to 3 mic. long and 0.7 to 1 mic. wide. See Fig. 17.

Synechoblastus nigrescens. Ascogonia 34 to 54 mic. below the surface, horizontal diameter 15 to 26 mic., vertical diameter 15 to 17 mic., 8-to 10-or more-celled, cells 6 to 8 mic. long and 3 to 4 mic. wide; trichogynes extending to and above the surface, 50 to 70 mic. long, cells 8 to 10 mic. long and 3 to 3.5 mic. wide; horizontal diameter of spermagonia 65 to 230 mic., vertical diameter 56 to 190 mic.; basidia 4-to 12-or more-celled, cells 3 to 5 mic. long and the same in width; spermatia 2 to 4 mic. long and 1 to 1.5 mic. wide.

Synechoblastus ohioensis. Ascogonia 90 to 225 mic. below the surface, horizontal diameter 16 to 37 mic., vertical diameter 16 to 30 mic., 7- to many-celled, cells 6 to 8 mic. long and 5 to 6 mic. wide; trichogynes passing directly or indirectly to the surface and 20 to 40 mic. above, where they are sometimes branched, 105 to 150 mic. long, cells 11 to 25 mic. long and 4 to 6 mic. wide; spermagonia submarginal, horizontal diameter 190 to 265 mic., vertical diameter 212 to 250 mic.; basidia 14- to 20-celled, cells 3 to 5 mic. long and 3 to 4 mic. wide; spermatia 3.5 to 5.5 mic. long and 0.8 to 2 mic. wide. See Fig. 25.

Collema pulposum. Ascogonia 155 to 600 mic. below the surface, horizontal diameter 16 to 39 mic., vertical diameter 13 to 57 mic., 5- to many-celled, cells 9 to 13 mic. long and 4 to 6 mic. wide; trichogynes extending 17 to 24 mic. above the surface, where sometimes branched, 155 to 625 mic. long, cells 8 to 54 mic. long and 6 to 8 mic. wide, distal cells much longer than others; spermagonia submarginal, horizontal diameter 65 to 240 mic., vertical diameter 75 to 240 mic.; basidia 7- or more-celled, cells 3 to 5 mic. long and 3 to 4 mic. wide; spermatia 1.5 to 4 mic. long and 0.5 to 1 mic. wide. See Figs. 15, 16, and 21.

Collema plicatile. Archicarps not seen; spermagonia numerous, commonly tinged with red, horizontal diameter 210 to 345 mic., vertical diameter 210 to 235 mic.; basidia many-celled, cells 5 to 6 mic. long and 2.6 to 5 mic. wide; spermatia 5 to 7 mic. long and 1 to 1.5 mic. wide, often slightly curved, located on the ends and sides of the basidia.

Collema microphyllum. Archicarps not seen; spermagonia submarginal, horizontal diameter 135 to 175 mic., vertical diameter 125 to 140 mic.; basidia several-celled, cells 4 to 8 mic. long and 4 to 5 mic. wide; spermatia 2 to 3 mic. long and 0.5 to 1 mic. wide.

Leptogium chloromelum. Ascogonia 60 to 95 mic. below the surface, horizontal diameter 18.5 to 24 mic., vertical diameter 26.5 to 29 mic., many-celled, cells 8 to 10 mic. long and 3 to 5 mic. wide; trichogynes not seen; spermagonia submarginal, horizontal diameter 60 to 210 mic., vertical diameter reaching 250 mic.; basidia 4-to 8-or more-celled, cells 2 to 6 mic. long and 3 to 5 mic. wide; spermatia 2 to 5 mic. long and 0.5 to 1.3 mic. wide. See Figs. 19 and 22.

Leptogium pulchellum. Ascogonia about 65 mic. below the surface, horizontal diameter about 14 mic., vertical diameter about 17 mic., 8-or more-celled, cells 7 to 8 mic. long and 5 mic. wide; trichogynes passing indirectly toward the surface, not fully studied; spermagonia marginal or submarginal, horizontal diameter 85 to 135 mic., vertical diameter 90 to 120 mic.; separate basidia not found; spermatia 2.5 to 3.5 mic. long and 1 to 1.5 mic. wide.

Leptogium lacerum. Ascogonia about 80 mic. below the surface, horizontal diameter about 18.5 mic., vertical diameter about 24 mic., many-celled, cells nearly isodiametrical; trichogynes not seen; spermagonia submarginal, horizontal diameter 60 to 135 mic., vertical diameter 70 to 120 mic.; spermatia 2.6 to 5 mic. long and 0.75 to 1 mic. wide.

Note. Only spermagonia which reached nearly to the surface and contained spermatia were measured. However, some of the sections may not have passed through the center of the spermagonium. This doubtless makes some of the minimum measurements too small.

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EXPLANATION OF PLATE III

Fig. 1. A section through the thallus of *Leptogium pulchellum*, showing the plectenchymatous cortex above and below and the mycelial medulla within. The algal-host chains are shaded. x 435.

Fig. 2. A similar section through the thallus of *Leptogium tremelloides*, highly magnified to show the close plectenchymatoid interweaving of the medullary hyphæ. x 1,000.

Fig. 3. A section showing a hypha and a portion of the thickened plectenchymatous cortex below an apothecium of *Leptogium pulchellum*. x 1,000.

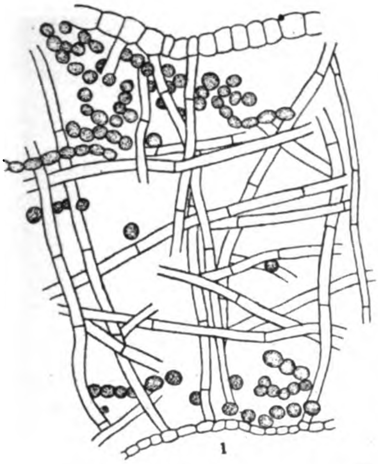
Fig. 4. Four cells of the upper plectenchymatous cortex of *Leptogium chloromelum*, isolated by maceration, but still cohering to the hyphæ from which they were cut off. x 1,000.

Fig. 5. A portion of a section of *Leptogium pulchellum* cut through the thickened plectenchymatous cortex below an apothecium, macerated, but the isolated cells still showing somewhat of the usual arrangement in vertical rows. x 1,000.

Fig. 6. A section through the thallus of *Synechoblastus flaccidus* to show a plectenchymatous cortex over a limited area above and closely packed hyphæ, forming a palisade over a limited area below. The horizontal lines above and below indicate the limits of the algal-host colony. x 875.

Fig. 7. Another section of *Synechoblastus flaccidus*, showing roughly isodiametrical cells cut off at the dorsal and the ventral surfaces, but not plainly plectenchymatous. x 875.

Fig. 8. Another section through the thallus of *Synechoblastus flaccidus*, taken from a region where there was little of the peculiar modification, but showing toward the center above two isodiametrical cells cohering in plectenchyma-like fashion. x 875.



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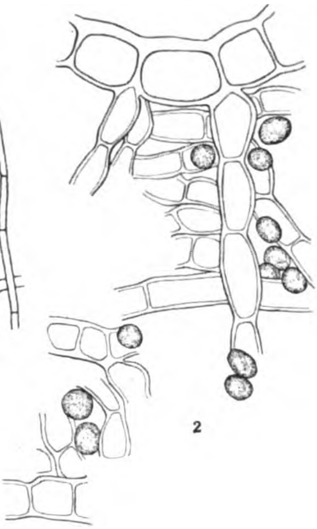

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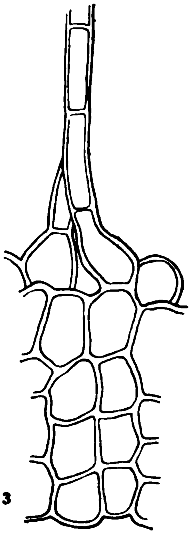

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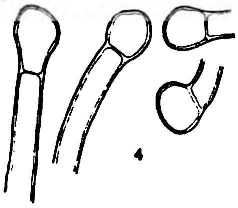

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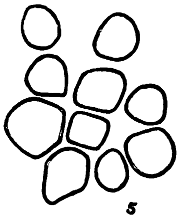

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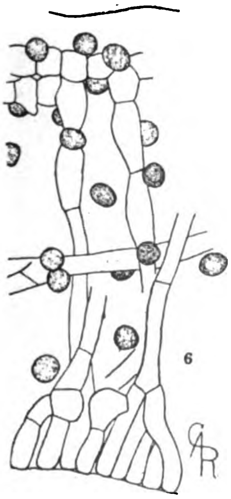

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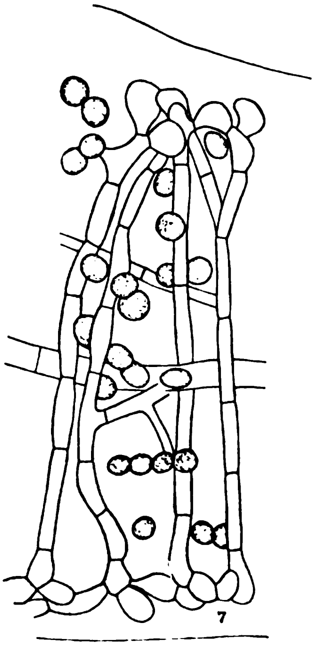

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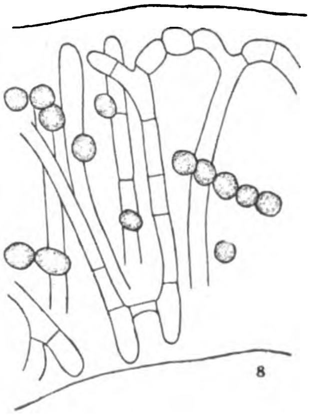

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EXPLANATION OF PLATE IV.

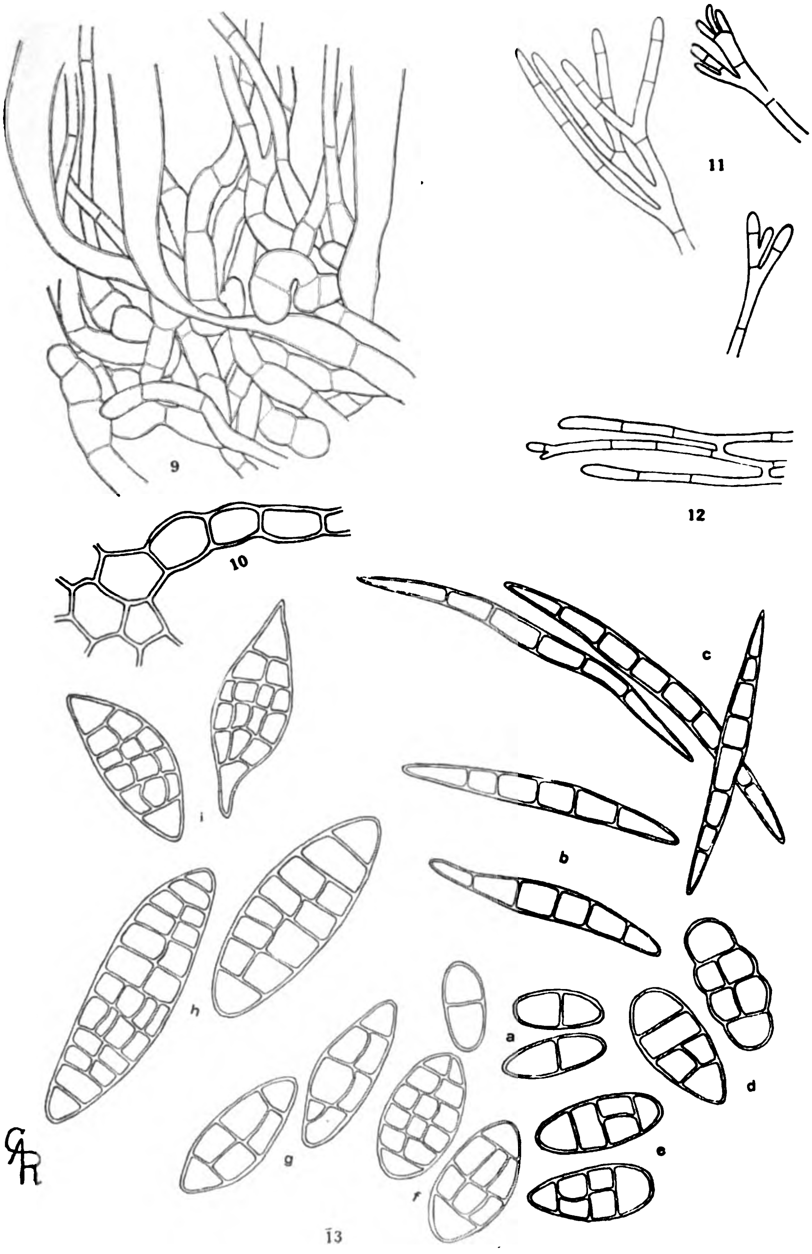
Fig. 9. A section through an apothecium of *Collema pulposum,* showing a portion of the hypothecium of interwoven hyphæ below and the lower portions of three asci and several paraphyses above. x 1,000.

Fig. 10. A portion of a section showing a few cells of a medullary hypha and three cells of the plectenchyma in the lower portion of the hypothecium of *Collema microphyllum.* x 1,000.

Fig. 11. Three types of branching of paraphyses in *Synechoblastus pycnocarpus.* x 580.

Fig. 12. Three paraphyses of *Synechoblastus nigrescens,* showing two of the bridge-like anastomoses sometimes seen in this species and a branch arising from the middle paraphysis. x 580.

Fig. 13. Types of spores found in the *Collemaceae;* a, 2-celled spores of *Synechoblastus ohioensis;* b and c, several-celled spores of *Synechoblastus flaccidus* and *Synechoblastus nigrescens;* d, e, f, g, h, and i muriform spores of *Collema pulposum* (d), *Collema microphyllum* (e), *Collema furvum* (f), *Leptogium plectenchymum* (g), *Leptogium lacerum* (h), and *Leptogium pulchellum* (i). x 1,000.



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EXPLANATION OF PLATE V.

Fig. 14. Internal reproductive organs in a member of the *Collemaceae* collected at Fayette, Iowa. Parts of two ascogonia at the left and two trichogynes passing toward a group of male reproductive bodies at the right. x 1,000.

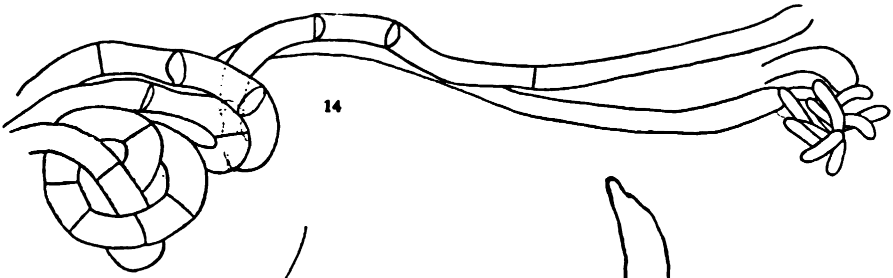
Fig. 15. Sixteen trichogynes of *Collema pulposum* seen projecting above the surface of the algal-host colony within one field of the microscope. x 580.

Fig. 16. A single archicarp of *Collema pulposum* from the same material from which Fig. 15 was taken. x 1,000.

Fig. 17. The tip of a trichogyne of *Synechoblastus flaccidus* branched more than usual. x 580.

Fig. 18. The coiled ascogonium of *Synechoblastus pycnocarpus,* with a portion of the trichogyne above and a portion of the supporting hypha below. x 580. Note how this differs in form of coil and form of cells from the archicarp of *Collema pulposum* shown in Fig. 16.

Fig. 19. The coiled ascogonium and portions of the supporting hypha and the trichogyne of *Leptogium chloromelum* for comparison with similar structures from other members of the *Collemaceae* shown in Figs. 14, 16 and 18. x 580.



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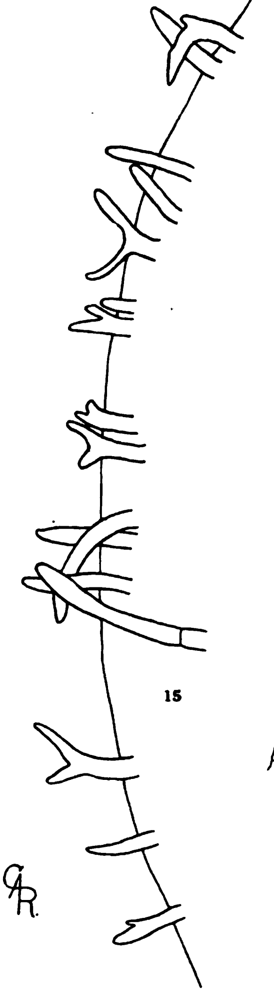

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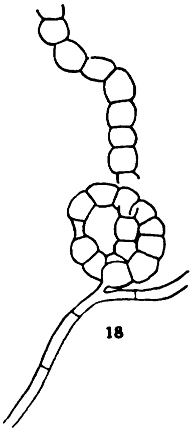

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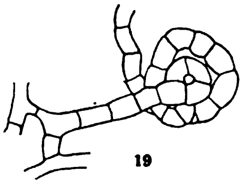

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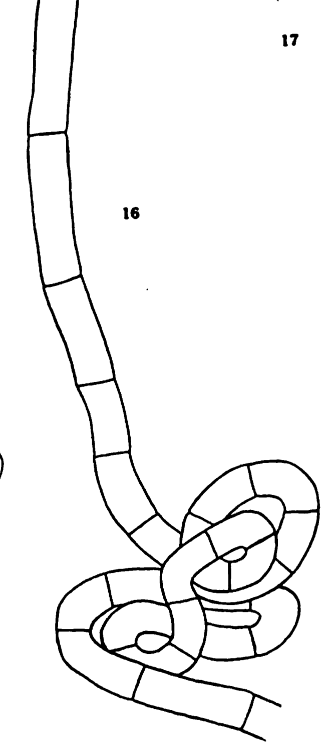

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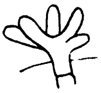

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EXPLANATION OF PLATE VI.

Fig. 20. Three groups of internal male reproductive organs from a *Collema*-like plant collected near Peebles, Ohio. x 1,000. Note how these male cells compare in form and size with the spermatia in Figs. 21, 22 and 23, drawn to the same scale of magnification.

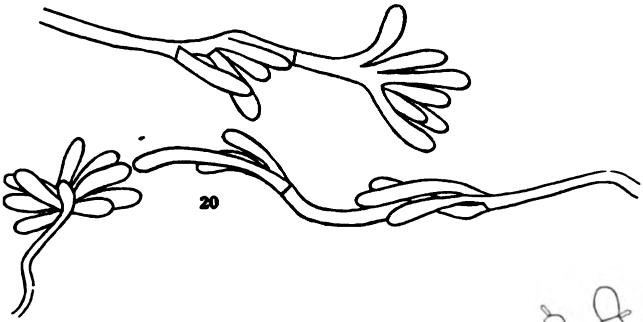
Fig. 21. Portions of three basidia of *Collema pulposum,* showing five spermatia attached. x 1,000.

Fig. 22. Portions of two basidia of *Leptogium chloromelum,* showing four spermatia attached. x 1,000.

Fig. 23. Portions of four basidia of *Collema microphyllum,* showing ten spermatia attached. x 1,000.

Fig. 24. Portions of three basidia of *Synechoblastus pycnocarpus,* showing twelve spermatia attached. x 870.

Fig. 25. A vertical section through a spermagonium of *Synechoblastus ohioensis,* showing the ostiole, many basidia, numerous spermatia, some attached and others free in the cavity of the spermagonium, hyphæ surrounding the spermagonium, and a few chains of cells and two free heterocysts of the algal host x 580.



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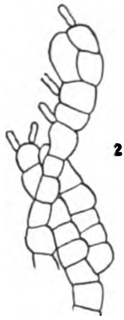

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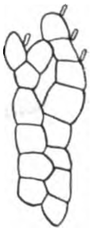

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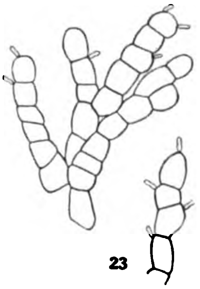

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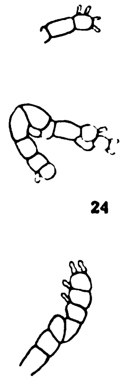

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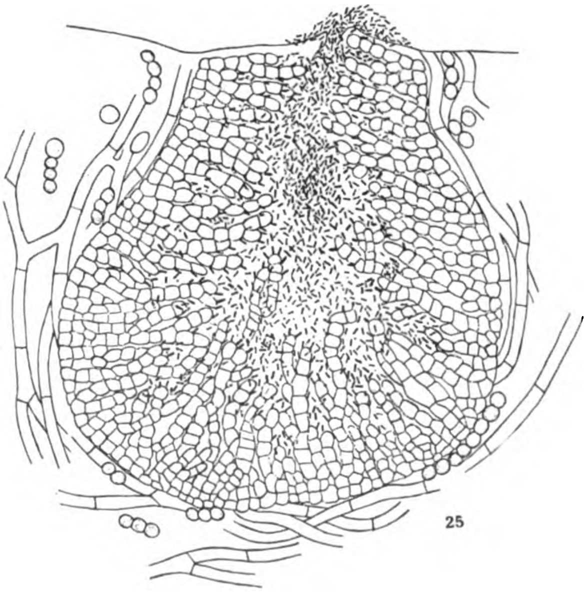

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